

ROSIDS (MALVIDS): MALVALES

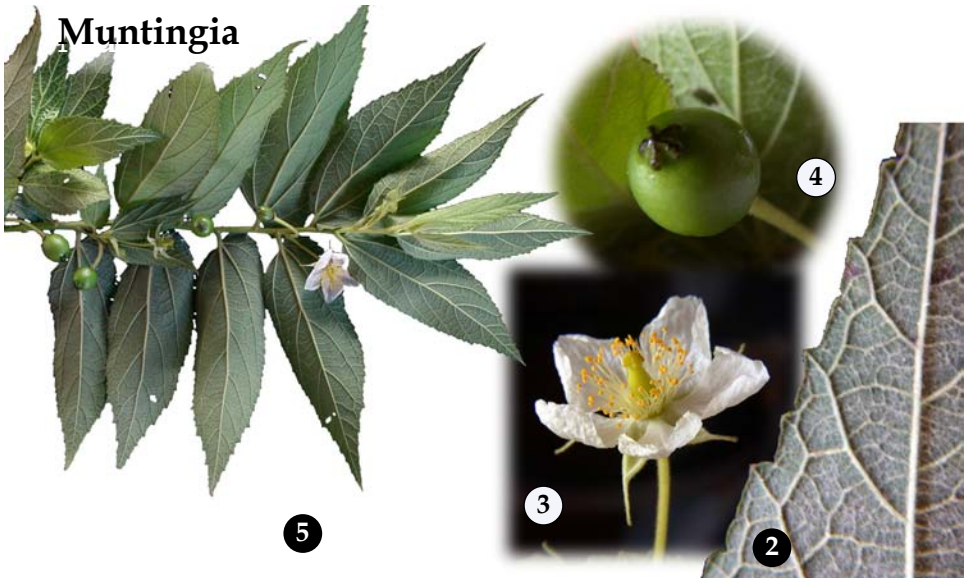
MUNTINGIACEAE

MUNTINGIA. *Muntingia* is one of three monotypic genera of tropical American trees that have been demonstrated to lie outside the Malvaceae proper, and probably sister to the entire clade, sometimes segregated in a new family, the Muntingiaceae¹. *Muntingia calabura* is not native to Asia and only casually cultivated, but it has widely naturalized and is now one of the most abundant roadside plants in the more seasonal parts of Asia. It was introduced into Philippines as *manzanita* from Mexico, perhaps in the late 19th century, and then found its way to Malaya and the mainland during the early 20th Century.

¹Bayer, C., et al. 1998. Taxon. 47: 37-42.

Muntingia is similar to the Malvaceae in general and to *Grewia* in particular in the fibrous character, symmetric leaves borne on a short unswollen stalk with what appear to be stipules, the strongly toothed margin, open five-part flowers, and numerous spreading stamens.

The node in fact is odd and in need of careful developmental study. The entire twig is strongly two-faced. The 'stipules' are little more than elongate awl-shaped appendages, one much longer than the other, but whether they are associated with the leaf or with the axillary bud is unclear. The small compact floral branch develops well above the normal axillary position. While the plants are obviously sticky, this is from long thin gland-tipped hairs and not from the mucilage characteristic of the Malvaceae. The stigma is oddly lumpy and start-shaped. The flowers are held erect above the branch; the mature red fruit hangs below the branch.



Muntingia calabura, native to tropical America, and widely naturalized in Asia; 1, the long leafy branches bear the flowers singly above the axils; 2, the margin is strongly toothed, each tooth irrigated by a nerve that ends in a gland; 3, the flower bears numerous free stamens; the fruit is odd in the star-shaped stigma; the fruit matures to a bright red color, sweet flesh with numerous seeds.

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ROSIDS (MALVIDS): MALVALES

MALVACEAE

NAME: From the genus *Malva*, the classical name of the European mallow.

OVERVIEW: A large and varied family of great ecological and economic significance, with roughly 4300 species in 250 genera. Although the family is roughly

cosmopolitan in distribution, and includes several crops of the warm parts of the northern latitudes such as okra and cotton, the family is especially rich in tropical trees and shrubs. Lianas are relatively few in species, but these, such as *Byttneria*, are often exceedingly abundant.

The modern practice of treating a single large family renders the Malvaceae more heterogeneous, but perhaps no more so than many other large families. General features of the family are adequately represented by the common cultivated *Hibiscus*. The leaves are typically in a

spiral, the base with three to five strong spreading nerves, the margins toothed; stipules are large and persistent, the leaf stalk is swollen at the upper end, prominently so in the large heavy leaves of the tropical trees, not so in the fleshy leaves of *Hibiscus*. Mucilage and strong fibers characterize the entire vegetative body. The flowers are recognized by the five-part valvate calyx and the five-part spirally contorted corolla; the stamens are many, the filaments often bundled and fused in one way or another. The ovary is five-chambered with hairs inside and covering the surface of the seed.

A new phylogenetic structure to the family was one of the early applications of molecular data¹⁻⁵. That work is far from complete and more extensive sampling is still required since many genera have shifted their placement based on molecular data alone, and so it is not possible to render a complete family arrangement at present. Another short-coming of the present structure is that the strongly supported groupings are not yet themselves arranged in any decisive order. In the present volume, I follow the subfamily arrangement of Bayer *et al.*⁶ with the exception of segregating the durians from *Helicteres* and placing them in their own unnamed group.

Throughout the wet tropics, the Malvaceae include several kinds of lofty trees, and yet they do not match the dipterocarps for overall abundance. Many Malvaceae are small fast-growing shrubs (*Colona*, *Triumfetta*) or medium trees (*Pterospermum*, *Hibiscus*) of the roadside, thoroughly different in ecology from the Dipterocarpaceae. There is a strong tendency toward the deciduous habit, and this is often retained in trees of the lowland habitats, such as *Heritiera elata*.

A few notes on pollination are given under the relevant genera, but as with so many tropical trees, definitive information is inadequate for generalizations.

The family has several big trees with wind-dispersed fruit or seeds. The fruits of *Schoutenia* are winged by expansion of the five calyx lobes, while the wings of *Pentace* and *Scaphium* are from the fruit wall. The effect with regard to population structure is comparable, large numbers of saplings in a dense shadows beneath the mother trees. In most durians and some species of *Sterculia* and *Leptonychia* the seeds bear a soft aril, and the saplings are widely scattered in the forest.

The family analysis in series Families and Genera of Vascular Plants is an excellent introduction⁶. It organizes the genera and subfamilies in the modern fashion with notes on the 250 genera in the world. For the trees of Borneo, you might consult the study by Peter Ashton⁷, which provides descriptions of the living trees and notes on edaphic ecology. During the 1950s, A.G. Kostermans contributed much to the taxonomy of the genera of Malvaceae with a series of detailed publications. However, they are, for the most part, exceedingly hard to find in our region outside of a few research libraries. I reference only three of the latter works here, but they can provide citations to the earlier works^{8,9,10}.

FIELD RECOGNITION: MALVACEAE

The bark, trunk and twigs are often stringy, fibrous and gummy, sometimes with wavy fishnet pattern.

Leaves are basically spiral often twisted to alternate in a plane.

The leaf margin is often toothed, the teeth often with glands.

Stipules are paired, lateral, usually big and obvious, sometimes falling off early.

The leaf stalk is typically longer than 1 cm and kneed on the upper end, less often or both ends but then the upper usually longer and more pronounced.

Most commonly, the leaf blade is strongly 3-5 nerved

Stellate hairs are common, and/or scales of silver, copper, or gold, and/or a glaucous bloom on the lower leaf surface.

FIELD CONFUSION

Euphorbiaceae, especially some *Mallotus*, and those species with alternate leaves and 3-nerved base, long kneed petiole, and stipules. The leaves themselves differ in that the petiole pulvini are shorter, not mucilaginous. (See the comparison plate under Euphorbiaceae.)

The other main source of confusion lies in the varied genera that have a 3-nerved leaf blade. Most of these, such as those of the old Urticalean families like *Trema* and *Celtis*, lack a pulvinate leaf stalk, while trees such as *Ficus* show various non-Malvalean characters such as white exudate, an encircling stipule, scabrous micro-costate venation.

The leaf stalk of many Dipterocarpaceae is nearly identical to that of, e.g., *Durio* and *Neesia*. The dipterocarps also share with the Malvales conspicuous stipules; they are nonetheless easy to recognize through the leaf nervation that is characteristic of the several genera, and they are resinous rather than mucilaginous

¹Alverson, W., *et al.* 1998. American Journal of Botany. 85: 876-887.

²Baum, D. *et al.* 1998. Harvard Papers in Botany 3: 317-332.

³Alverson, W., *et al.* 1999. American Journal of Botany. 86: 1474-1486.

⁴Bayer C. *et al.* 1999. Botanical Journal of the Linnean Society. 129: 267-303.

⁵Tate, J. *et al.* 2005. American Journal of Botany. 92: 584-602.

⁶Bayer C. *et al.* 2003. Families and Genera of Vascular Plants. 6: 225-311.

⁷Ashton, P. 1988. Manual of Non-Dipterocarp Trees of Sarawak. Volume 2. Dewan Bahasa dan Pustaka, Malaysia.

⁸Kostermans, A. 1953. Journal of Science Research Indonesia 2: 13-23.

⁹Kostermans, A. 1959. Penerbitan, Madjelis Ilmu Pengetahuan Indonesia 1: 1-121 & Reinwardtia 4: 465-583.

¹⁰Kostermans, A. 1958. Reinwardtia 4: 357-460.

Phylogeny of Malvaceae

The modern view of the Malvaceae echoes the 19th century practice of aligning these many genera in a single family, an arrangement in contrast with the 20th century practice of limiting the Malvaceae to the immediate associates of *Malva*, while recognizing three other major families: Sterculiaceae, Tiliaceae and Bombacaceae, all four in a narrowly conceived Malvales. The change is not merely the raising or lowering of taxa along the hierarchy - which is trivial - but represents a real change for the better by the realignment of so many genera. Durians finally break away from the utterly different *Bombax* trees, *Grewia* is segregated from *Pentace* and allies while *Tilia* itself is properly isolated, and the very distant elaeocarps are altogether dismissed from the Malvaceae.

Ten clades equivalent to subfamilies are usually recognized. All ten are represented with at least one species of tree in tropical Asia, and only *Tilia* is not treated in this volume, but even one species of that genus reaches the northern extremity of Vietnam. Below, I provide an arrangement of the subfamilies, listing only those genera represented by trees in our region. The new arrangement is based largely on molecular studies cited in the family introduction. Note that although the individual groupings are relatively strong, their relationship to one another remains unclear. I provide informal group names following our more conspicuous genera of trees, and provide the formal subfamily beside each group name.

GENUS	NOTES
GREWIA GROUP - Grewioideae - 25/770, Pantropical.	
<i>Grewia</i>	90, Paletropics, especially Africa.
<i>Microcos</i>	60 India to Australia.
<i>Colona</i>	SE. Asia, India to the Solomons.
<i>Trichospermum</i>	30, Pantropical.
LEPTONYCHIA GROUP - Byttnerioideae - 20/650, Pantropical, chiefly American.	
<i>Leptonychia</i>	28, Africa, Africa, 3 in Asia.
<i>Byttneria</i>	132, Pantropical, herbs and lianas, maybe 1 tree in Asia.
<i>Commersonia</i>	9 Australia, 1 widespread, weedy in Tropical Asia.
<i>Abroma</i>	5, Asia to Australia.
<i>Kleinhovia</i>	1, Indian Ocean to Polynesia.
STERCULIA GROUP - Sterculioideae - 12/430. Pantropical.	
<i>Sterculia</i>	Pantropical; 19 in Borneo.
<i>Heritiera</i>	30, Africa and Asia.
<i>Scaphium</i>	12, Mainland SE Asia to Borneo. .
<i>Pterocymbium</i>	15, Tropical Asia.
<i>Pterygota</i>	12, Pantropical.
<i>Firmiana</i>	12, Africa and Asia.
PENTACE GROUP - Brownlowioideae - 8/70, mainly Palaetropics.	
<i>Pentace</i>	25, tropical Asia.
<i>Brownlowia</i>	20, India to the Solomon Islands.
<i>Diplodiscus</i>	7, Philippines, Sabah, Malaya, Sri Lanka
<i>Jarandersonia</i>	3-5, Borneo.
<i>Berrya</i>	3, India, Sri Lanka to Pacific.
<i>Pityranthe</i>	2, 1 Sri Lanka, 1 in S China and Mainland SE Asia.
PTEROSPERMUM GROUP - Dombeyoideae - 8/70, especailly Africa to Iddia.	
<i>Pterospermum</i>	20, India to China and the Pacific.
<i>Burretiodendron</i>	4, tropical China and northern Mainland SE Asia
<i>Eriolaena</i>	17, India to China.
<i>Excentrodendron</i>	2, China and Vietnam.
<i>Paradombeya</i>	1 China. 1 Myanmar and Thailand.
<i>Schoutenia</i>	9, N Thailand to Java and N. Australia; not Philippines.
TILIA GROUP - Tilioideae - 3/50, N Temperate, Central America.	
<i>Craigia</i>	2, China, Vietnam.
HELICTERES GROUP - Helicteroideae, in part - 6/150, Pantropical.	
<i>Helicteres</i>	60, tropical Asia and America, 3-5 in dry seasonal tropical Asia
<i>Reevesia</i>	18, S China and E Himalayas, 1 S to Vietnam, cultivated.
DURIO GROUP - Helicteroideae, in part - 4/50, tropical Asia.	
<i>Durio</i>	30, Sundaic Region.
<i>Neesia</i>	7, tropical Asia
<i>Coelostegia</i>	5, tropical Asia
<i>Kostermansia</i>	1 tropical Asia
HIBISCUS GROUP - Malvoideae -, 78/1800, cosmopolitan.	
<i>Camptostemon</i>	2, Borneo, Philippines.
<i>Hibiscus</i>	250, pantropical, maybe 12 trees in tropical Asia.
<i>Thespesia</i>	Pantropical, several in New Guinea, 2 in tropical Asia.
<i>Kydia</i>	1, India to Mainland SE Asia.
BOMBAX GROUP - Bombacoideae - 12/120, tropical, especially Africa and America.	
<i>Bombax</i>	20, Pantropical
<i>Ceiba</i>	American, 1 in Africa, cultivated in tropical Asia.

☞ - *Grewia* Group - ☞

Subfamily Grewioideae

A heterogeneous group of 25 genera and 770 species, characterized by free sepals, without floral nectaries, the stamens usually free and without staminodes. We might also mention *Triumfetta* and *Corchorus* as herbs and scrambling ruderal shrubs.

GREWIA. [Commemorates Nehemiah Grew, English scientist, pioneer in microscopy and author of the first text on plant anatomy, d. 1712.] Index Kewensis lists a devilish 666 names under *Grewia*. The genus is badly over described and there are far fewer species than the 280-300 suggested in The Families and Genera of Vascular Plants *loc. cit.*, which treats the genus in combination with *Microcos*. The number is probably closer to estimates in Flora of China: 90 species in *Grewia* and 60 in *Microcos*. The two genera have similar distributions: rich in Africa and then eastward to Australia and the Pacific. They are unsatisfactorily distinguished as follows: *Grewia* by leaves with evenly toothed margins, relatively large flowers in small axillary inflorescences, dehiscent fruit, often four-lobed; *Microcos* with entire leaves, dense much-branched and more or less terminal inflorescences of small flowers, a blunt style and baccate fruit. Certainly, in the extreme, the two types of trees are very different and there is likely a strong clade surrounding each of the main types, but there is also much heterogeneity.

Most of the species of the Sundaic Region are in *Microcos*, with *Grewia* itself all but negligible in the lowland equatorial forest. *Grewia* is perhaps best represented in tropical Asia by two species. The first is the scrambling liana *G. laevigata* (previously well-known as *G. asiatica*). The second is a small tree, *G. multiflora*, (previously known in Java as *G. glabra* and *G. oblongifolia*). *Grewia multiflora* is an abundant small tree of secondary forests in dry-seasonal parts of tropical Asia from India to Australia and including the Philippines, where it is known as *danglin*, but is sparsely found in the Sundaic Region. It is quickly recognized by the long leaf stalk swollen in the upper part, by the leaf margin with serrations to the base, and by the two- or four-lobed fruit. In places, the flowers open wide with spreading yellow petals (see the photograph in FERNANDO *loc. cit.*), but in some places, as illustrated here, the flowers never seem to open, yet every flower forms a fruit. Another 10 to 15 species may be found in Mainland SE Asia, and all are in need of taxonomic revision by a local student working with the variation in the field. Of particular interest is the sexuality of the flowers, because there are varied claims of unisexuality and dioecy.

MICROCOS. [Burmah's Greek translation for 'coconille', little coconuts, for the small hard stones.] About 60 species, especially abundant in the lowland forests. For its relation to *Grewia*, see the notes above. Known as *chenderai* in Malaya and *bunsi* in Sarawak. The leaf is not always immediately recognizable as a Malvaceae because of the short and apparently unswollen leaf stalk.

When the stalk is long, as in *M. cinnamomifolia*, the swollen pulvinus is obvious. When it is short, it seems as though the leaf stalk is all pulvinus and no stalk. In some of the Thai and Indo-Chinese species we find a tendency toward an asymmetric leaf base, although not so pronounced as in, for example, *Colona*.

The genus is ecologically broad with abundant trees of the dry-seasonal lands and also many species of the lowland Sundaic Region. It includes some fast growing plants of the full sun, such as the common canopy tree *M. paniculata* of Mainland SE Asia, but also many shade-loving trees of the forest. The species of the lowland equatorial forest need further work to clarify their ecological position. They are bird-dispersed and widespread within the forest, by no means exclusive to gaps, and yet they grow relatively quickly, often as much as 0.5 cm DBH per year. As adults they rarely exceed 30 cm DBH.

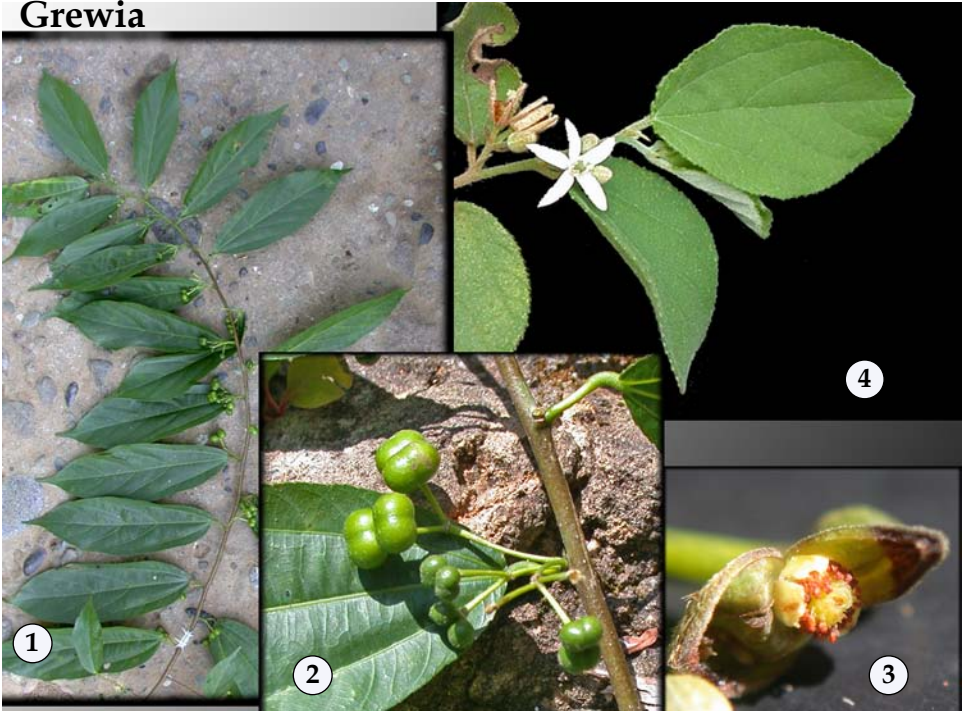
Microcos stylocarpa can be found in most of the Philippines lowland wet forests, and often in sufficient abundance and sufficiently large size to form a small timber market. The stipules are variably obscure, small and awl-shaped or wide and much lobed.

COLONA. [Commemorates Christopher Columbus, Colon was the family name at birth.] About 30 species, tropical Asia generally, but mainly in dry-seasonal forests, India and South China (two species) to the Pacific, with maybe a dozen in the Philippines. They are uncommonly encountered in the everwet parts of the Sundaic Region and never within the forest understory.

These are small to medium sized trees, essentially a *Grewia* with winged fruit. There is a tendency for the leaf base to be asymmetric and invaginated, sometimes strongly so. *Colona discolor* and *C. serratifolia* are among the more abundant trees in open places and forest margins in Philippines, while *C. flagrocarpa* is a tree of dry dipterocarp forests from Central Thailand northward. *Colona auriculata* of Mainland SE Asia is often not more than 1-2 m tall, a great arched herbaceous frond, the architecture of which deserves more attention. Perhaps the small stature has made the winged fruit less useful, because here the fruit are unusually large, rounded, and densely hairy, the wings are often little more than ridges. *Colona nuba* is equally abundant in Vietnam; the bark is the most popular of the several Malvaceae that are dried and used in *Areca*-chewing, adding both mucilage and a spicy flavor.

TRICHOSPERMUM. [Greek, hairy seed.] An odd weedy genus of three Neotropical species and an uncertain number of species in the Paleotropics, perhaps 10-20, chiefly in New Guinea and eastward. Four species are found in the Philippines, but only one, *Trichospermum javanicum*, occurs further west, a widespread and abundant shrub of open places in dry seasonal lands. The floral sexuality needs clarification; the flower is similar to *Grewia*, but larger and with many seeds each of which bears a tuft or ring of spiny hairs.

Grewia



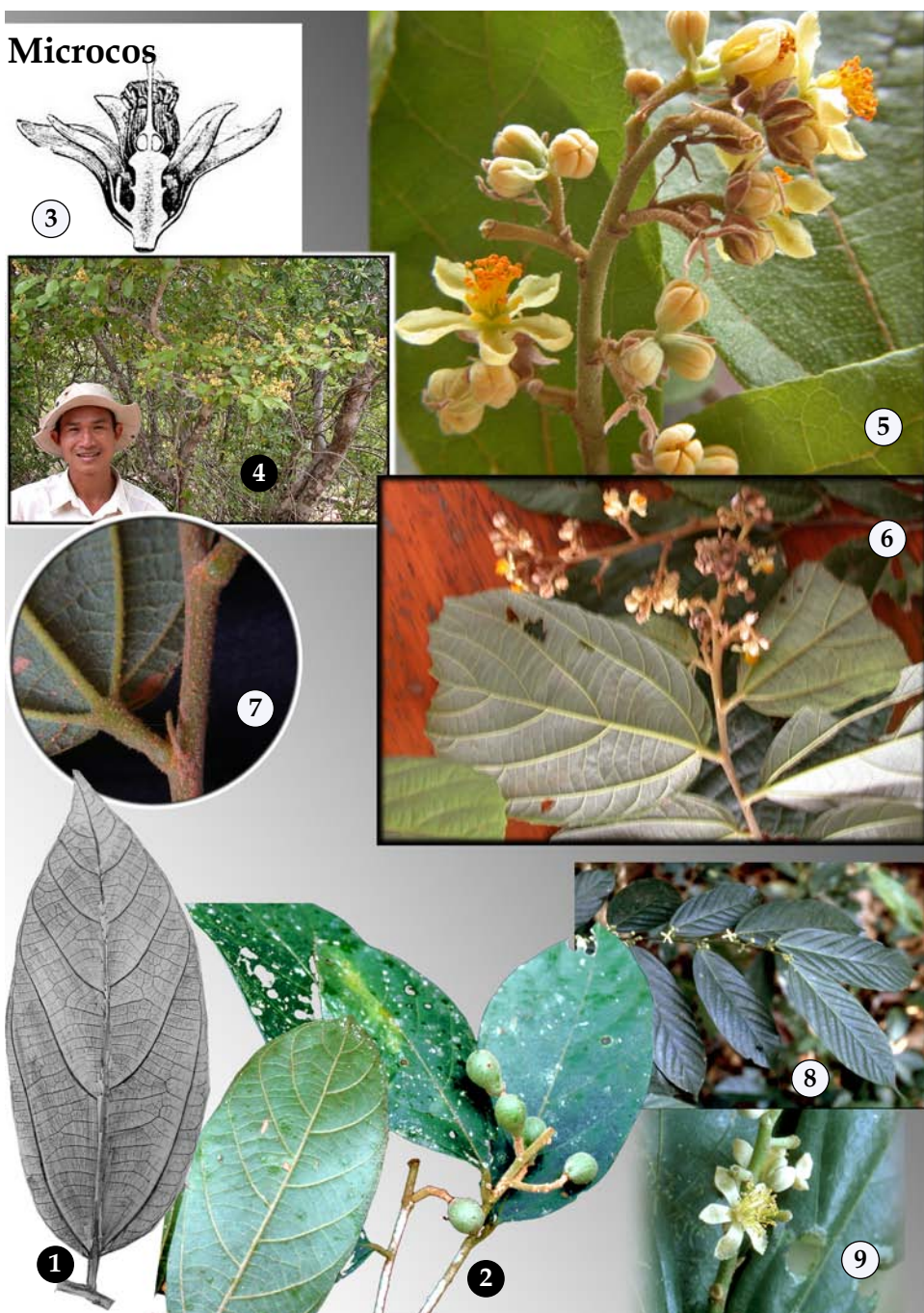
Grewia multiflora, Philippines; 1, long leafy branches with axillary clusters of fruit; 2, note the long twice swollen leaf stalk and four-lobed fruit, odd in the family; 3, the flowers, barely three mm across, never opens among these roadside plants in the Philippines; 4, an unidentified *Grewia* from the dry coastal planes of central Vietnam.

Microcos

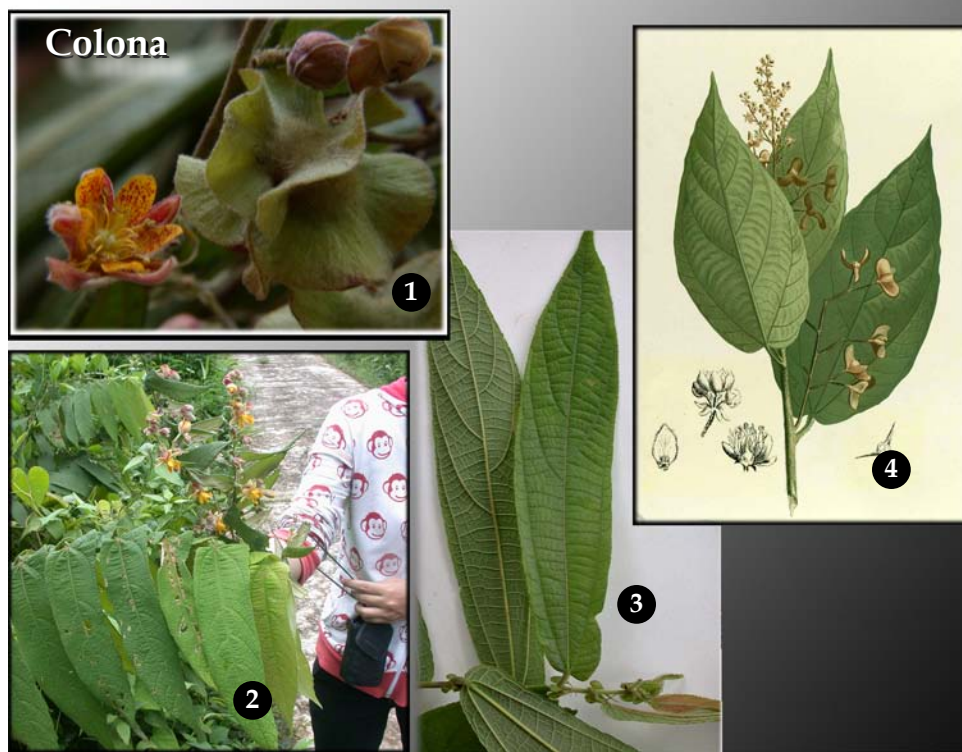


Microcos. 1-2, *M. cinnamomifolia*, Sarawak, (camera lens in lower right for scale), can be confused with *Anisophyllea* and other trees with strongly 3-nerved blades, but note the long pulvinate leaf stalk; 2, the flowers are small but otherwise typical of the genus; 3-5, *M. stylocarpa*, Philippines, the open flowers are about 10 mm across, the fruit about 15 mm across and typical of the simple drupe that characterizes the genus, but perhaps more fleshy and sweet than in most species. (Photograph 3, © Leonardo L. Co; 4-5, © Ulysses Ferreras.)

Microcos



Microcos. 1, *M. fibrocarpa*, Sarawak, a pencil tracing of the leaf, 28 cm long, illustrating the nervation typical of the genus, the short stalk, strong 3-nerved base and entire margin; 2, *M. blattaeifolia*, Malaya, the large elliptic blade with short leaf stalk and strong 3-nerved base is typical of many species, the fruit are small drupes; 3, drawing of floral details; 4-5, a small tree in Vietnam, allied with the *M. paniculata*-*M. tomentosa* group, complex in both biology and nomenclature; 5, flowers with numerous stamens, the petals much reduced within the spreading cup-shaped sepals; 6-7, a small tree from dry coastal Vietnam, again falling within the messy *M. paniculata*-*M. tomentosa* group, but here with unusual and distinctive truncate and bilobed blade; 7, the leaf stalk typical of the genus, short and essentially pulvinate throughout its length, with a small stipule pair; 8-9, *M. antidesmaefolia*, Malaya, thin blade and numerous lateral nerves, white petals. (Diagram 4 from BALLION *loc. cit.*)



Colona. 1-2, *C. auriculata*, Vietnam coastal lowlands, flower and fruit with negligible wings; 2, the habit of single arching stem with large pendent leaves and numerous flowers; 3, *C. evrardii*, Vietnam, winged stipules, asymmetric 3-nerved leaf base; 4, *C. serratifolia*, Philippines, showing habit, flower and winged fruit. (Illustration from BLANCO *loc. cit.*)

♂♂ - *Leptonychia* Group - ♀♀ Subfamily Byttnerioideae

This subfamily has been recently reorganized based on molecular work¹¹. It now includes 26 genera and 650 species, pantropical, but especially rich in South America. The flowers are bisexual with calyx and corolla, five or more stamens. The complex hooded petals seen in *Theobroma* are evidently pleiomorphic and the smaller flatter or scale-like petals are derived. Most of these genera were formerly in the Sterculiaceae. Included here is the Neotropical *Theobroma cacao*, the source of chocolate, sometimes in home gardens, especially in the Philippines, a few plantations in Malaysia, but the quality of the seed is low.

LEPTONYCHIA. [Greek, thin nail-shaped, in reference to the petal.] A genus chiefly of Africa with nearly 40 species; about three in tropical Asia. These are common and relatively abundant species that include small understory trees and medium-sized lower canopy trees. The leaves are entire with a three-nerved base, borne on a long stalk that is sharply pulvinate above. The flowers are borne in small axillary cymes; they bear five se-

pals and five petals, neither showy, the filament of the stamens are united in the basal half. The stamens are in three series with fertile stamens in the middle ring and sterile stamens outside and in. The fruit is one-three-celled capsule, thin walled and breaking open when dry to reveal brightly arillate seeds.

Leptonychia caudata is a small tree with thin papery leaves and shiny black-violet twigs. It is abundant and widespread in lowland equatorial forests from Malaya, Sumatra and Borneo; the same name is applied broadly even though the small trees vary in detail from place to place. *Leptonychia banabaensis* is an abundant lower canopy tree in the Philippines.

ABROMA. [Greek, inedible, uncertain reference.] A genus of only two species. The first is *Abroma fastuosa* of Australia and New Guinea. The second comprises small weedy shrubs of variant forms that are usually lumped under the name *Abroma angusta*. It is found in most of tropical Asia from the Mainland to Australia. The Malay is *rami sengat*. It never much exceeds three to four m in height; the branches arch outward to display the broad leaves. The leaves and stems are covered with bristly irritating hairs. It is sometimes cultivated under the name *devil's-cotton*. The flower and the fruit are both odd. The large maroon corolla forms something of a chamber and

¹¹Whitlock, B. *et al.* 2003. Systematic Botany. 26: 420-437.



Trichospermum involucre, from Cuernos Mts., Negros Island, Philippines; note the flat fruit with persistent calyx, mealy white lower leaf surface. (© Leonardo L. Co).

is presumed to be fly-pollinated. The fruit is a large star-like hollow capsule.

COMMERSONIA. [Commemorates P. Commer-son, d. 1775, French botanist and explorer.] The genus

includes nine species of Australia and one widespread weedy shrub on tropical Asia. The leaves bear an unequal invaginated base. The inflorescence is a variously positioned cyme; the calyx bears five broadly triangular lobes; the petals number five, are concave at base and end with a long strap-shaped appendage at the tip. The five fertile are opposite the petals and alternate five staminodes. The fruit is dehiscent five-valved densely bristled capsule.

KLEINHOVIA. [Commemorates C. Kleynhoff, German physician, d. 1777.] This is a genus of a single well-known species, *Kleinhovia hospita*, widespread from the islands of the Indian Ocean to Polynesia, found in most places with a dry seasonal climate. The Malay is *temehau*, and it is known in the Philippines as *tanag*. The flowers bear five pink calyx lobes, and five strongly unequal petals, the stamens arranged in an arch. The fruit is an inflated papery capsule with a few seeds, one-two per locule, the entire capsule seemingly wind dispersed, but each warty seed with a small food body, and so is perhaps secondarily ant dispersed.

MELOCHIA. [From an Arab plant name.] A genus of 68 species, chiefly of the American tropics, a few species in Africa and Madagascar, and two or three in tropical Asia, weedy shrubs, rarely more than two m tall, *Melochia corchorifolia* and *Melochia umbellata*. These are small shrubs, leaves spirally arranged, entire with toothed margins, three-nerved, prominent stipules. Bright pink flowers are clustered in axillary particles; five sepals, five petals, five stamens fused as a tube, the ovary five-celled, each cell with two ovules. The fruit is a dehiscent cap-

Leptonychia



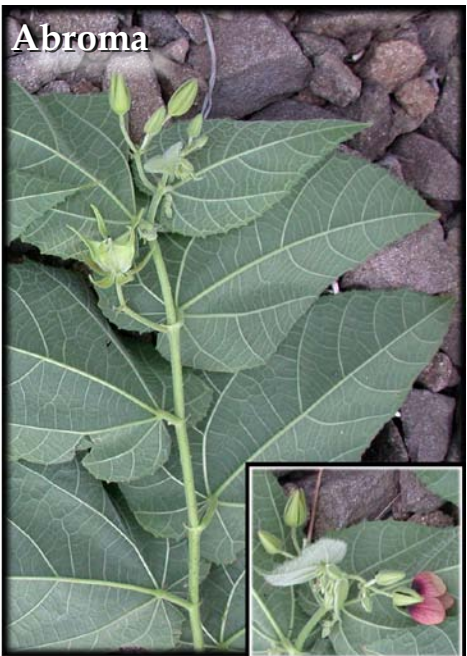
Leptonychia. 1-3, *L. caudata*. 1, leaf tracing from Lambir; 2-3, small tree with immature fruit, Pasoh, large seed and orange aril; 4-5, *L. banahaensis*, Luzon Philippines; 10 cm DBH tree, mature fruit with black seed and red aril. (Photographs 4-5 © Leonardo L. Co).



Kleinhovia hospita, Philippines; 1, habit; 2, leaf; 3, leaf base with leaf stalk swollen in upper portion and without laminar glands; 4, flower, about 7 mm across; 5-7, inflated capsule in stages of maturation.



Commersonia bartramia; above, mixed fruit and flower, Philippines; below right, leaf tracing from Sarawak, Borneo; below left, line drawings. (Photograph © Leonardo L. Co; floral line drawings from VIDAL *loc. cit.*)



Abroma angusta, small roadside tree in northern Luzon, Philippines; asymmetric leaf (juveniles are peltate), toothed margin, note the large inflated fruit; inset shows the red-petaled flower.

sule. Usually in waste places and forest margins. (Not illustrated.)

WALTHERIA. [Commemorates German botanist and physician A. Walther, d. 1746.] A genus of maybe 50 species in the American tropics and a widespread pantropical weed, *Waltheria indica* (sometimes *W. americana* is treated as distinct, sometimes in synonymy.) In all events, these rarely exceed two m in height. They are well-established along sandy shores of the tropical world. (Not illustrated.)

☞ - *Sterculia* Group - ☞
Subfamily Sterculioideae

A strongly monophyletic group of medium sized to large trees, distinguished by unisexual flowers that lack petals but possess an androgynophore, a combination unique to Sterculioideae¹². The leaf is three to five-nerved, usually simple, but can be lobed or palmately compound (rarely reduced to a single leaflet, then appearing pinnate nerved). The group is mainly Paleotropical and especially important in tropical Asia; most of the tropical American genera formerly in Sterculiaceae are now in other subfamilies, and the Sterculioideae are represented in America but little more than a few species of the pantropical *Sterculia* and *Pterygota*. *Sterculia* is by far the largest and most heterogeneous genus and may not prove to be monophyletic with respect to the other 12 small genera. Three genera of Australian trees form a distinct clade: *Argyrodendron*, *Francisodendron* and *Brachychiton*, few species reaching west to New Guinea.

STERCULIA. [Latin, dung, after the fetid smell of the flowers in some species.] The Malay is usually *kelumpang*. The more common names in Borneo are *melebu*, *biris* and *buah ayan hantu sebayan*. Peter Ashton *loc. cit.* recounts: "According to Iban tradition the fruit was originally green, but was visited by the Spirit of the Dead, hence its name *buah ayan 'antu sebayan*; this accounts for its subsequent brilliant color, that makes it so conspicuous, hanging on its slender stalk against the dark green of the forest undergrowth."

Sterculia is a large and very heterogeneous assemblage of about 150 species with a worldwide tropical distribution. Most species are small trees, a few are large canopy trees, these with plank buttresses. The bark is smooth in small trees, gray to brown, or in large trees fissured or flaky. Growth is often markedly episodic with long internodes and lateral branches built sympodially in a terminalian fashion. The leaves of our native species are simple and entire with a strong or weak three-(five) nerved base; many are obovate with a short or long leaf stalk, double-kneed, very straight and stiff, strongly kneed where it joins the blade. The flowers are generally unisexual, the plants monoecious, although all the details of reproduction need more field observation. The calyx bears five lobes, sometimes in a basket-shaped form where the tips

remain fused, these said to be fly-pollinated, the petals wanting, the anthers sessile at the apex of a slender staminal tube. The five carpels are free, borne on a short gynophore. The typical fruit is a dehiscent capsule, the walls leathery red or yellow in color, with velvety black seeds pendent from the edges. The fruit are often enough relatively long persistent on the ground and these can aid the identification of larger trees.

In lowland equatorial forests we find three fairly common types. First, very large trees with entire well-stalked leaves; second, are trees that are similar but very small, sometimes no more than 1 cm DBH; third are a few species with a *schoepfbaum* habit, a short tree with a single thick stem that bears a dense cluster of nearly sessile leaves. In this last type, you may need to look closely to note the small three-nerved base. In the strongly dry seasonal forests, trees with palmately invaginated leaves are common. The most commonly cultivated species is probably *Sterculia foetida*, a name that rightfully suggests the unpleasant odor of the flowers.

HERITIERA. [Commemorates Charles L. L'Heritier, temperamental and controversial French aristocrat, botanical patron, murdered in Paris, 1800.] A genus of about 35 species distributed from tropical Africa to tropical Asia where it is most prevalent, and at least in the form of the littoral mangrove, *H. littoralis*, eastward to Australia and the Pacific. We find nine species in Malaya, 11 in Borneo. In the Philippines, other than *H. littoralis*, we find only *H. sylvestris* as a widespread national endemic, while *H. javanica* of the Sundaic Region reaches no farther north than Mindanao. The forest trees are usually with plank buttresses and cylindrical boles that rise tall and straight 30-50 m before branching in great hemispherical crowns.

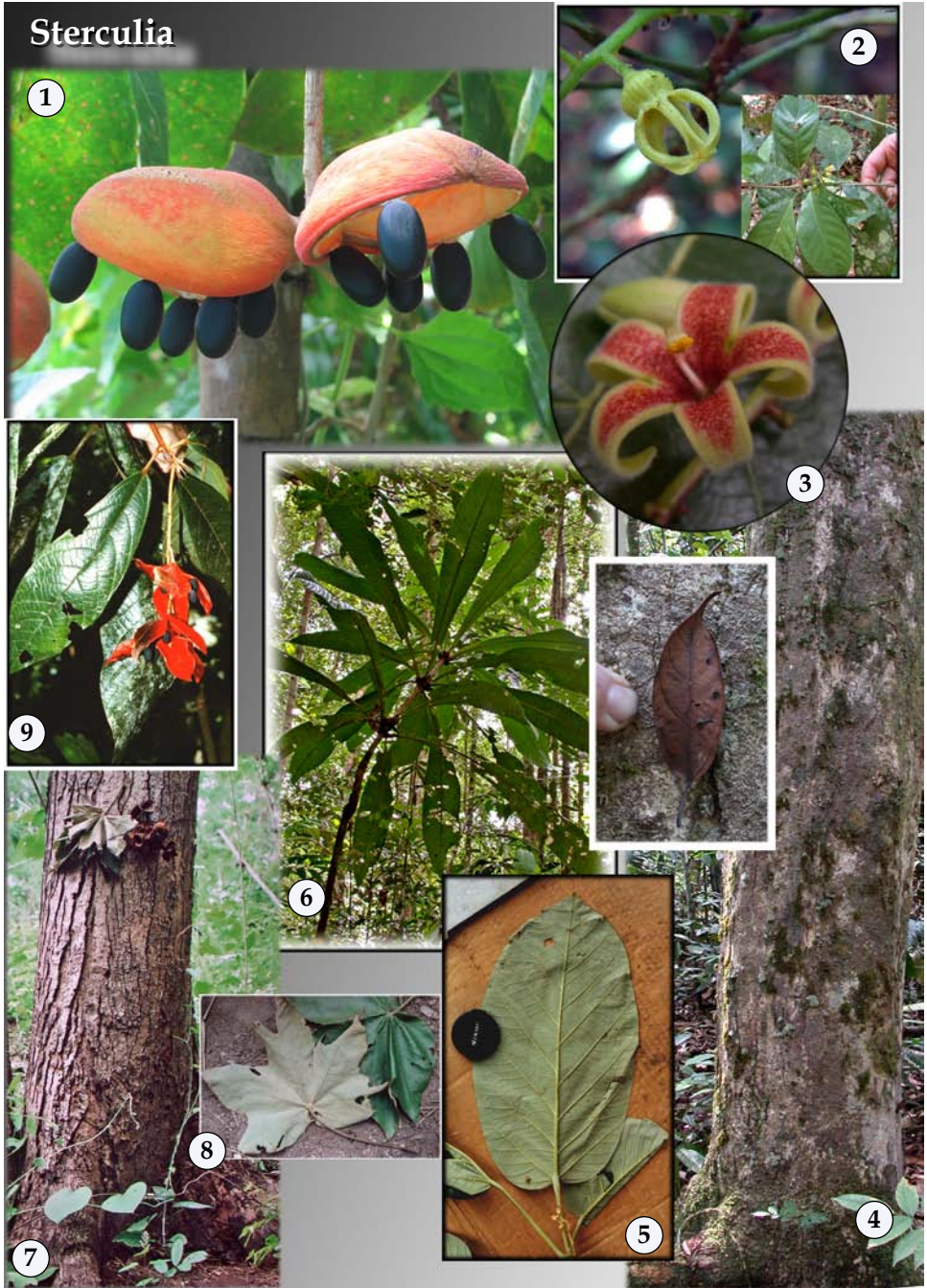
The Malay and Iban names are often shared with *Sterculia*, such as *biris* and *megkulang*, while the distinctive and widespread coastal tree, *H. littoralis* is usually called *dungun*.

The leaf blade is curious in many *Heritiera*. The blade of juvenile plant is palmately lobed or even palmately compound, and this condition may persist as the tree reaches as much as 30 cm DBH, whereas in the mature plant the blade can be simple and palmately nerved, as in *Heritiera elata*, or reduced to a single lobe of the compound blade as in *H. simplicifolia*, and then the blade appears pinnately nerved. If you note the articulation between leaf stalk and blade you can see that this is essentially a compound leaf with a single leaflet.

The leaves open in an interesting fashion. The compound blade of the very young leaflet is held in line as the leaf emerges from amidst the stipules, then the stalk relaxes and the blade folds backwards as the stalk lengthens, eventually the stalks spreads from the twig and the leaflets of the blade opens.

Heritiera is distinguished by small unisexual flowers, calyx more or less bell-shaped with four to five lobes, petals wanting, the male flower with an androgynophore of eight to 10 anthers that dehisce by longitudinal slits. The stamens number five and alternate with sterile an-

¹²Wilkie, P. *et al.* 2006. Systematic Botany 31: 160-170.



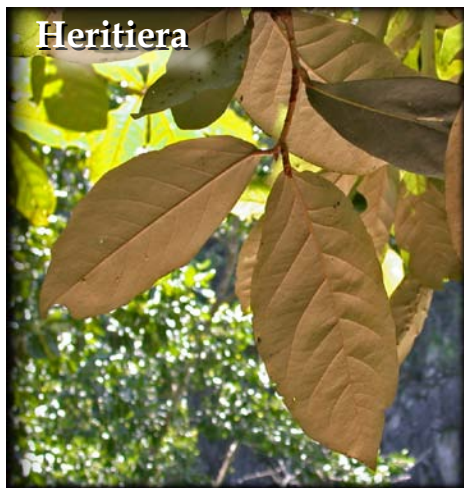
Sterculia. 1, fruit of *S. coccinea*, characteristic of the genus, dry follicle, dehiscent in valves with black seeds attached to the margins; 2, small understory *Sterculia*, related to *S. coccinea*, loosely spiral leaves, tips of the calyx lobes touching; 3, flower of the cultivated *S. foetida*, flowering when leafless, colored petal-like calyx; 4, *S. parvifolia*, Pasoh Forest, Malaya, a large tree with exceedingly small leaves, the leaf base 3-nerved; 5, an unidentified *Sterculia* from Lambir, Sarawak, large soft leaf, the leaf base invaginated, small inflorescence; 6, *S. bosei*, a small understory tree at Lambir Hills, Sarawak, leaves large, in interrupted whorls along a single upright stem; 7-8, *S. cordata*, Huai Kha Khaeng, Thailand, large tree with palmately invaginated blade; 9, *S. rubiginosa*, Lambir Hills, Sarawak, understory tree with characteristic fruit.

thers; the carpels mature as dry papery fruit typically with a wing, but some without.

Little is known of the reproductive biology of these species, and the fresh flowers of the large trees have rarely been studied in any detail. For at least a few species, the germinating seeds produce mucilage in the habit of *Scaphium*.

SCAPHIUM. [Greek, a boat, reference to the shape of the winged fruit.] *Kembang semangkok* is the Malay, in reference to the great quantity of mucilage that comes from a seed when placed in water. In Sarawak you hear the name *kepayang babi*, in reference to the palmate shape of the juvenile leaf, which is like the *kepayang* tree (*Pangium edule* of the Salicaceae), but that name is also used for the entirely different *Mezzettia* (Annonaceae) in reference to the fruit.

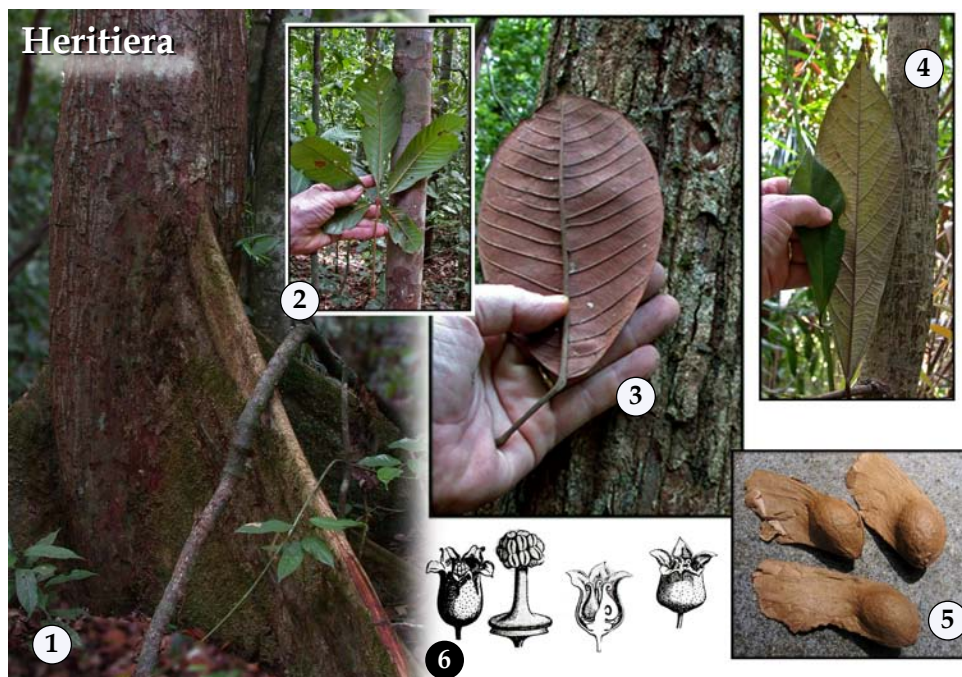
Scaphium includes at least 10 species that are currently the subject of revision by Peter Wilkie of the Royal Botanical Garden in Edinburgh. They include several core species of the lowland equatorial forest, especially *Scaphium macropodum* which is found consistently and abundantly throughout the Sundaic Region. Borneo claims perhaps five or six species while two species reach into the seasonally dry forests of Mainland SE Asia. The genus does not extend to the seasonally dry forests further east, and the Philippines does not currently recog-



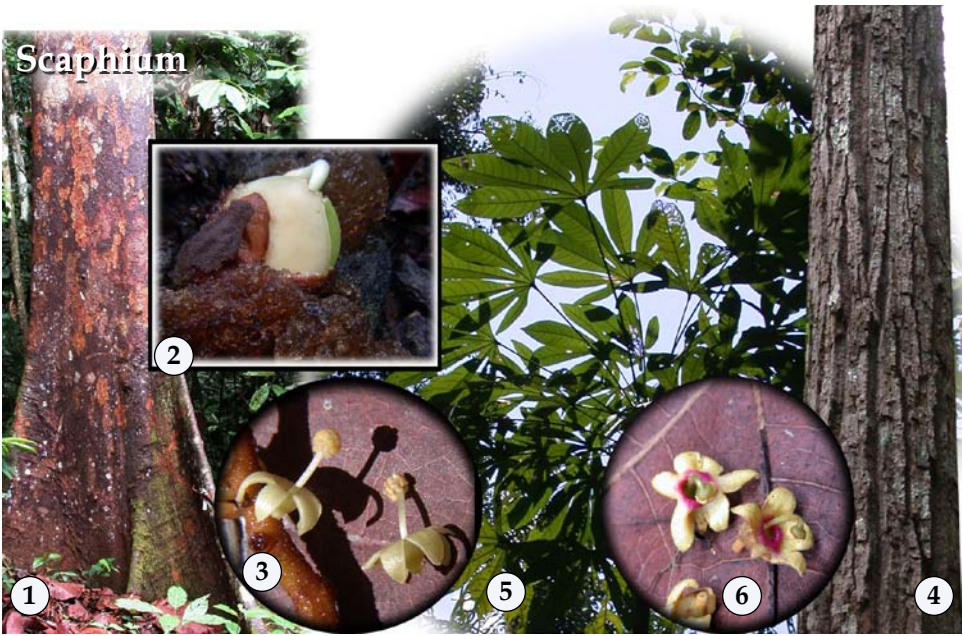
Heritiera littoralis, golden lower leaf surface and 3-nerved base; ocean-side forest, Palawan, Philippines.

nize a native species, although the genus it is expected in eastern Mindanao and western Palawan.

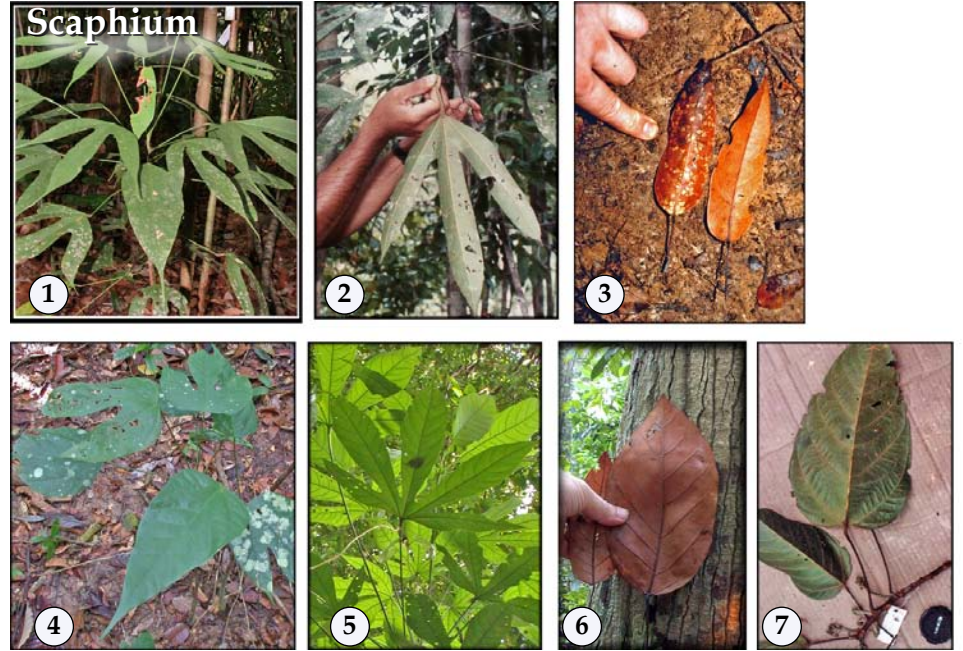
They are fairly large trees of the lower to mid canopy, with plank buttresses, short or broad by species, the bark variably red brown and mottled or distinctly and deeply V-fissured (especially *S. macropodum*). The leaf shape from seedling to adult varies in the degree of invagina-



Heritiera. 1-3, *H. simplicifolia*, Pasoh Forest, Malaya, typical of the large forest species with fibrous reddish brown bark and short sharp buttresses, 2, the juvenile leaf, palmately compound; 3, the adult leaf is a single leaflet, strongly pinnate but lacking 3-nerved base; 4, *H. excelsa*, here a juvenile from Lambir Hills, Sarawak, silver-golden below with a 3-nerved base, appears black from below the canopy; 6, the fruit of the timber tree *H. sylvatica*, Philippines; 7, illustration of staminate and pistillate flowers. (Photograph 5, © Ulysses Ferreras; illustration from BAILLON *loc. cit.*)



Scaphium. 1-3, *S. linearicarpum*, Pasoh Forest, Malaya; 1, the mature tree, 52 cm DBH above the narrow buttresses, and bark dipped red and brown; 2, the seed germinating in a mass of water-retaining mucilage; 3, staminate flowers, about 4 mm across; 4-6, *S. macro-podum*, Pasoh Forest, Malaya; 4, the characteristic deeply furrowed bark of the mature tree, 31 cm DBH; 5, the array of deeply digitate leaves of the sapling; 6, pistillate flower with arched stigma.



Scaphium. Changes in leaf form with maturation. 1-3, *S. borneensis*, Lambir Forest, Sarawak; 1, sapling, the first leaf is entire; 2, at 2 cm DBH the leaf is 3-lobed; 3, the leaf of the mature tree is a small entire blade with a 3-nerved base; 4-7, *S. macropodum*; 4, the seedling leaves change from entire to trilobed; 5, at 2 cm DBH, the leaf is deeply digitate with 5 or 7 lobes; 6-7, at maturity the leaf is entire with a 3-nerved base; the base is either rounded (6, Pasoh Forest Malaya) or square to nearly invaginated (7, Lambir Forest).

tion. The first leaf pair are nearly round while the seedling leaves take the lanceolate shape of the adult. When the saplings reach one-two m tall they begin to develop the deeply invaginated blade that provides such a distinctive feature of the lowland Sunda Shelf forest; this leaf shape is replaced by the mature leaf once the diameter reaches eight cm or so, or when the tree emerges into full sun. The three strong basal nerves are always retained.

The stalk is long and strongly swollen above. The flowers are markedly reduced in size, hardly more than 3–5 mm across, with a five-lobed calyx and no corolla, presumably unisexual, the trees evidently monoecious with separate staminate and pistillate inflorescences, the gynoecium with two to five carpels. The carpel walls expand rapidly after fertilization, splitting to form a big green papery boat that lacks the 'nose' found in *Pterocymbium*. When the seed contacts the ground and is moistened, the seed coat swells and generates a mass of clear mucilage. The saplings are almost always abundant and conspicuous around a mother tree.

PTEROCYBIUM. [Greek, winged-boot, a clumsy description of the elegant clawed fruit.] This genus is close to *Scaphium* and represented by no more than five or six species, found in the Sundaic Region and



Scaphium longipedicellatum, Lambir, Sarawak, the leaf and a winged seed behind.

also in seasonally dry places in Mainland SE Asia as far north as Doi Suthep, Thailand; in the Philippines it is found as far north as northern Luzon and east to western New Guinea. *Pterocymbium tinctorium* is especially widespread and abundant. The Malay name is *keluak*, and in the Philippines it is known as *taluto*.

These are large, elegant trees, entirely deciduous, the bole with short, rounded buttresses, the bark is a light rusty orange-brown in color, sometimes mottled with black patches and pock marked with 10 cm diameter circles. It is a fast-growing gap species, soft-wooded and stinky. *Pterocymbium* differs from *Scaphium* in the thin papery leaves that fall black and in the strongly deciduous habit. The leaf blade of *Pterocymbium* retains an entire outline from seedling to adult. The calyx is much larger than in *Scaphium*, and the seeds do not exude a gelatinous mass. The wing, together with the off-center seed, is similar to *Scaphium* in that it creates a strong helicopter motion as it falls. But it differs in the nose-like extension at the base, which evidently exaggerates the lift, because the seeds are remarkably good fliers.

FIRMIANA. [Commemorates Count Karl von Firmian, governor of Lombardy, Austria, d. 1782.] *Firmiana* is a Paleotropical genus of perhaps 15 species, distributed from Africa to the Pacific, and especially in dry-seasonal forests. It is taken here to include the those Asian species transferred to the essentially African genus *Hildegardia*.

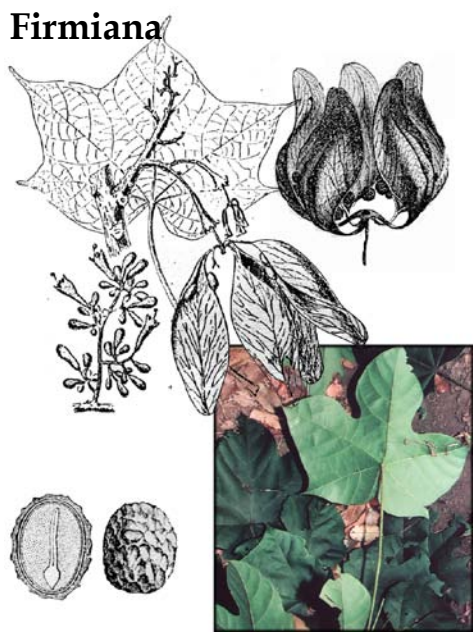
Firmiana simplex, the Chinese-parasol-tree is widely cultivated in cooler places. A big tree with a heart-shaped blade, typically trilobed as a juvenile, from long leaf stalks. *Firmiana malayana* is a strongly deciduous tree that blooms and fruits after dropping its leaves. The Malay name as *mata lembu*. The natural distribution follows those parts of tropical Asia that are strongly dry seasonal, from Thailand southward to northern Malaya where it is abundant in places such as Penang Hill, and in west Java and Sumatra. It can be cultivated in less seasonal places, and several big trees are found in the Singapore Botanic Gardens. Borneo is generally too wet for it, but it curi-



Pterocymbium tinctorium. Left, Pasoh, Malaya, the mature tree in leaf; a drawing of the black fallen leaf; and a single seed with the peculiar wing; right, the leafless canopy in flower, Palawan, Philippines, a close up of the fallen flowers.



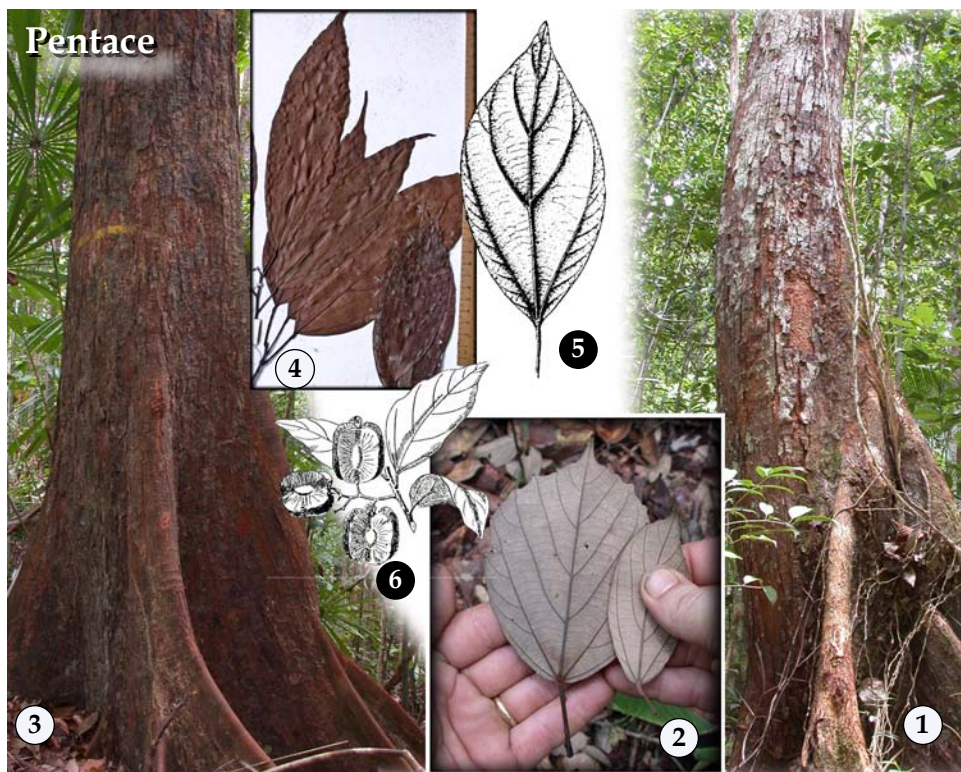
Pterygota alata, illustration adapted from BLANCO *loc. cit.*, photograph from Lambir, Sarawak, winged seeds approximately 5 mm long, fruit to 7 cm.



Firmiana malayana, the drawing of twig in flower and fruit from BRANDEIS *loc. cit.*; the drawing of fruit and seed from BAILLON *loc. cit.*; photograph of the leaf from Huai Kha Khaeng, Thailand.

ously shows up growing on limestone outcroppings in the west part of the island. Northward into the Philippines the genus is patchy with *Firmiana philippinensis* found in Pangasinan, Luzon, and Merrill's *F. merrittii* (often treated under *Hildegardia*) from Mindoro. It is a large deciduous tree, reaching a height of 30 m, and a trunk diameter of 90 cm DBH.

PTERYGOTA. [Greek, winged seed.] *Index Kewensis* lists 25 names that represent maybe nine to 15 species, with a pantropical distribution, however the genus badly needs a new monograph. While obviously similar to both *Cola* and *Sterculia* it differs in the woody capsule bearing shortly winged seeds. In tropical Asia, these trees might be best treated at the moment as a single species, *Pterygota alata* (but commonly mentioned as *P. horsfieldii* following Kostermans) with a wide but patchy distribution from Sri Lanka to Mainland SE Asia, then to Java and New Guinea and patchily north in the Philippines from Mindoro to north west Luzon, and curiously along a single ridge on the Santubong Peninsula in Sarawak, but perhaps also to be found in Sabah. Ashton, (in the work cited above) described these as, "Magnificent trees with dense hemispherical emergent crowns, a pale mauve-gray shallowly fissured bark surface and with tall thin spreading convex plank buttresses." The seeds hardly seem capable of wind dispersal over significant distances. These interesting trees with their odd seeds,



Pentace. 1-2, *P. adenophora*, Lambir, Sarawak, the well-buttressed mature tree, the fallen leaves of variable size but typically white below and with gland-tipped teeth in the upper third of the margin; 3-4, *P. borneensis*, mature tree, 64 cm DBH; 4, herbarium sample, the leaves dry red-brown, with 3-nerved base; 5, line tracing of the leaf of *P. triptera*, about 6 cm long and white below; 6, drawing of the Indian species *P. burmmanica*, adapted from BRANDEIS *loc. cit.*

peculiar ecology and uncertain history have been rarely collected and never studied in the field. They certainly deserve better.

☞ - *Pentace* Group - ☞ Subfamily Brownlowioideae

The subfamily includes 80 species and about 8 genera, with different genera in different parts of the world. The genera of tropical Asia are restricted to the Old World. Most of our trees in this group are distinguished by a fused calyx (not free as in *Grewia*), the presence of petals and more than 5 free stamens (not many free, or fused stamens), and by an ovary with mostly fused carpels (not free as in the *Sterculia*).

PENTACE. [Greek, five-wings, as in the fruit of the type species.] *Pentace* is taken to be a small genus of perhaps no more than five species, but these trees are not so well-known as they should be, and there may be additional species. It ranges from India and Mainland SE Asia to Java and Borneo and the southern Philippines, equally at home in dry seasonal and in the ever-wet forest. These are medium-sized to large tree with large plank buttresses. The bark, hairs and scales vary by

species. The leaf blade is usually glaucous white below, the blade with three to five strong basal nerves, and in some species we find prominent glandular teeth in upper third of the blade margin. The leaf of juvenile plants often differs from adult: the juvenile with teeth, adult without.) The leaf stalk is generally long with a sharply swollen pulvinus at the upper end, and often bent. The inflorescence is a large and open panicle. The flowers are bisexual with a fused calyx and distinct corolla. The fruit is a dry indehiscent one-seeded capsule with three to 10 wings. *Pentace triptera* can be an enormous tree of two m diameter with numerous seedlings and saplings beneath the mother tree.

BERRYA. [Commemorates Dr. Andrew Berry, 19th century physician in Madras.] *Berrya* is a genus of perhaps six species, five narrowly distributed, but *B. cordifolia* from India and Sri Lanka to Mainland SE Asia and eastwards to Polynesia, but rare outside lands with a strong dry season. Most often these are trees of small stature, or at least they begin to flower at a small size. They differ from all the other members of the subfamily in our area by the absence of staminodes in the flower. The leaf is cordate and the stalk is hardly swollen at the apex. The fruit is a globose capsule of three valves, locu-



Berrya cordifolia, Saigon Zoo, Ho Chi Minh City, Vietnam.

licidally dehiscent, each valve with two erect wings, and each valve bearing one or two seeds. In India, *B. cordifolia* reaches a fairly large size and the hard red wood provides a small timber market.

BROWNLOWIA. [Commemorates Lady Brownlow, daughter of Lady Amelia Hume, a patroness of botany.] A group of perhaps 20 species, most are poorly known. The genus is distributed from India to the Solomon Islands. The mangrove species, *Brownlowia tersa*, is perhaps the most widespread, from India, to Thailand, Borneo and the sole representative of the genus in the

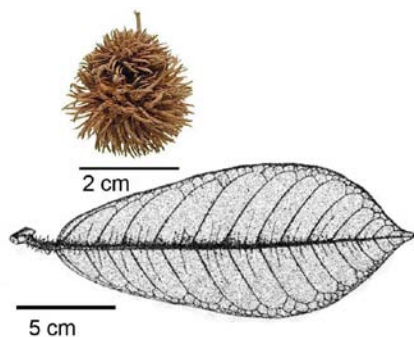
Philippines. *Brownlowia peltata* is the only species that may reach the lower canopy; it is notable in the strongly peltate leaf, and also odd in distribution, being known from the eastern half of Borneo and also Myanmar and Thailand. Otherwise these are small trees, narrowly distributed, especially in Borneo where more than a dozen are known. The leaves bear a white scaly lower surface, but unlike *Pentace*, the leaves of *Brownlowia* are usually without a toothed margin and are often peltate or deeply invaginated. The flowers are fairly ordinary: both calyx and petals present and in fives, stamens numerous either free or in five bundles, five staminodes. The ovary comprises three (or five) carpels joined by a common style, develops as a characteristic lobed and ridged capsule about two cm across, from which the carpels individually disperse, each with a single seed, evidently by water. The seeds are said to lack endosperm. Most of the species show a marked preference for swamps, streams, river banks or mangroves.

DIPLODISCUS. [Ashton suggests reference to the paired suborbicular anther cells.] *Diplodiscus* is a genus found widely from India and Sri Lanka to the Pacific, but with perhaps no more than seven species, although a few of these are locally significant. For example, *Diplodiscus paniculatus* is fairly common throughout the Philippines where it is known as *balobo*. It is also cultivated in Hawaii for the edible nut. The genus is distinguished in having a typically one-celled ovary that bears one or two wingless seeds. The leaf stalk is short, without a distinction between swollen and unswollen portion (as in the *Grewia* group), and usually an unequal and sometimes cordate leaf base. The summary by Bayer and Kubitski implies the blade is not three-nerved, but this is not so, although the lowermost pair of nerves are indeed thin and not strongly divergent.

Diplodiscus



Diplodiscus paniculatus, Philippines, leaves and detail of twig tip; line drawing of floral and fruit details from VIDAL *loc. cit.*



Jarandersonia. Below leaf of *J. spinulosa*; above, fruit of *J. clemensiae*. (Photograph of fruit from USDA-GRIN; leaf redrawn based on Ashton, *loc cit.*)

PITYRANTHE. This genus represents a new circumscription that combines *Pityranthe verrucosa* from Sri Lanka with the former *Hainania trichosperma*, now as *P. trichosperma*, the latter known from Guangxi, Hainan, Yunnan and at least Vietnam if not elsewhere in Mainland SE Asia. Small trees, the inflorescence is a terminal panicle of bisexual flowers. The stamens number about 20 and there is a whorl of five staminodes opposite the petals. The ovary is five-locular each with five ovules, usually only one develops as a seed; the fruit an angular dehiscent capsule. (Not illustrated.)

JARANDERSONIA. [Commemorates JAR Anderson, British botanist of Sarawak, noted for his studies of

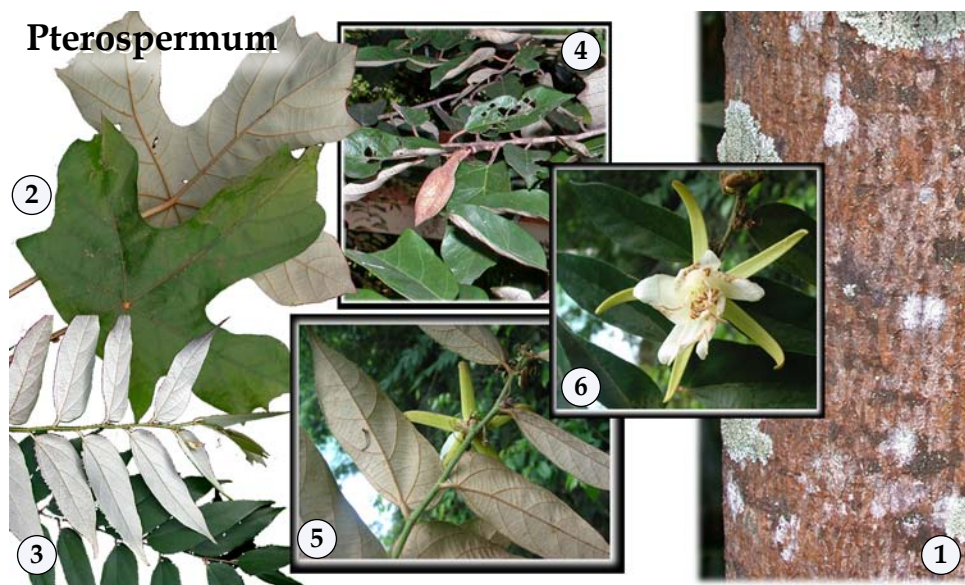
the peat forests.] This small genus of perhaps three-five species is restricted to Borneo, poorly known, a total of perhaps a dozen collections for the entire genus. It differs from *Diplodiscus* in having a prominently spiny fruit.

❧ - *Pterospermum* Group - ❧

Subfamily Dombeyoideae

A Palearctic subfamily with 20 genera and 350 species, with most of the diversity in Africa Madagascar, India and also Australia and west Pacific. In tropical Asia it is chiefly represented by *Pterospermum* growing in full sun and gaps, and *Schoutenia* as a canopy tree of the lowland equatorial forests. The group is distinguished by an epicalyx, free sepals, stamens fuse but without androgynophore. The subfamily is named after the largest genus, *Dombeya*, over 200 species of colorful and fragrant flowering shrubs, chiefly of Africa, known in horticulture as the tropical hydrangeas.

PTEROSPERMUM. [Greek, winged-seed.] These trees are famously variable in the often odd shape of their foliage, variable among saplings and also along branches in the same tree, a habit that has led to a great over-description of more than 80 basionyms recorded in *Index Kewensis* for the estimated 25-30 species. These trees are most abundant and diverse in the dry seasonal parts of tropical Asia; they not a usual member of lowland equatorial forests of the Sundaic Region, although several species are common in gaps and along river banks and patchily numerous in broken wet forests. There are about 15 species in Mainland SE Asia, two-three in Bor-



Pterospermum. 1-2, *P. diversifolium*, Philippines; 1, the trunk of a 21 cm DBH tree; 2, the peltate leaves are highly varied shape; 3, *P. obliquum*, Luzon, Philippines, with simple leaves but strongly asymmetric at the base; 4, *P. acerifolium*, in fruit, southern Vietnam; 5-6, *P. celebicum*, Luzon, Philippines, flower with 5 calyx lobes and the oddly twisted petals. (Photographs 5-6, © Leonardo L. Co.)



Pterospermum grandiflorum, Huai Kha Khaeng, Thailand, the variable foliage and the large woody capsule, that splits to disperse the small seeds.

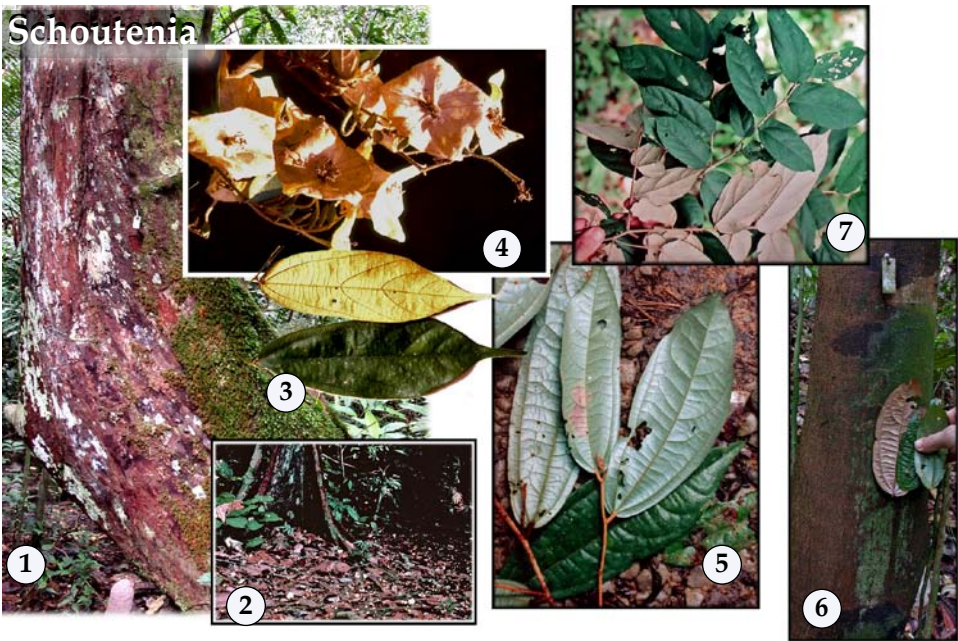
smooth to shallow fissured bark. The leaf surface is most often white below with stellate hairs. As mention, the leaf outline is highly variable, the base asymmetric and peltate especially in juveniles. The leaf stalk is short and neither pulvinate nor flexed. The flowers are relatively large and showy, white or yellow, the calyx of five thick sepals, that abscise at the base to form a collar around the fruit. The petals are narrow, often asymmetric and twisted, The fruit a five-valved woody capsule, rusty tomentose, the valves break apart to release the winged seeds.

SCHOUTENIA. [Commemorates WC Schouten, d. 1625, early Dutch circumnavigator.] About eight species, the genus characteristic of both the seasonally dry and everwet parts of tropical Asia from Mainland SE Asia to Java, Borneo, and east to N Australia. The leaves with a bright coppery or white lower surface look

neo, and six in the Philippines. The Malay names include *banyur* and *bayur* and in the Philippines as *balok*.

These trees are of medium stature and famously fast-growing, with short broad buttresses and a pink-brown

like *Pterospermum*, but *Schoutenia* differs in the lack of a corolla and in the ovary reduced to a single-seeded dry berry, the calyx is five pointed, fused at the base and persistent to serve as a dispersal wing. Pollen and molecular



Schoutenia. 1-4, *S. accrescens*, Pasoh, Malaya; 1, the spreading buttresses of a mature tree; 2, the winged fruit littering the ground beneath that same tree; 3, the golden lower surface and deep green upper surface of the fresh leaves; 4, the winged fruit; 5, *S. glomerata*, Lambir, Sarawak; 5, the leaves with silvery-blue lower surface; 6, leaves and trunk of the mature tree ; 7, *S. ovata*, of southern Vietnam.

data removes *Schoutenia* from *Grewia*-types and place it here.

The genus is centered in Malaya with six species, three of local distribution. The most widespread and abundant is probably *S. accrescens*, (with the Malay name *bayur bukit* applied with fidelity, at least by Forestry Departments), found from S Thailand to Borneo, neither the species nor the genus yet recorded from Philippines. This is a large tree, tall enough in the lowland forests to take advantage of the well-developed calyx-wing that facilitates wind dispersal. A species of the Sundaic Region of contrasting habit is *S. glomerata* of S. Thailand, Malaya and Borneo. It is a smaller shrub or tree with a more silvery lower leaf surface and a fruit in which the calyx wings are smaller, these dispersal probably by water. Two other species are found in Mainland SE Asia, *S. ovata*, (= *S. hypoleuca*) found in the Mainland, and then in Java and disjunctly in the two location is the Northern Territories of Australia. *Schoutenia peregrina* is found in N Thailand.

BURRETIODENDRON. [Commemorates Burret, author of the last monographic study of the family.] A small genus of four species, from Mainland SE Asia northward to tropical China. Differences with *Pentace* supposedly include unisexual rather than bisexual flowers, axillary rather than terminal inflorescence. The capsule is oblong, with a short stalk and five thin wings and is said to be loculicidally dehiscent with one seed in each of the five cells. Two species are usually segregated as the genus *Excentrodendron*, with *E. tonkinense* found at least in northern Vietnam. (Not illustrated.)

ERIOLAENA. [Greek, in reference to woolly calyx lobes.] Essentially a genus of N India and W China, poorly collected, but not uncommon, between eight and 15 species, with at least *Eriolaena candollei* southward in Mainland SE Asia. *Eriolaena* species are small deciduous trees, the leaves and twigs with stellate indumentum, the pretty yellow flowers are bisexual, calyx deeply cleft, lobes hairy on both sides, petals large, anthers numerous, fused at the base and of varying filament length, the ovary with a long style and five to 10 spreading stigmas develops as a woody dehiscent capsule, winged seeds numerous.

PARADOMBEYA. [Close to *Dombeya*.] A genus of two species; the name *Paradombeya burmanica* is used in Thailand for a rarely collected and poorly known tree. The better known tree is *P. sinensis*, restricted to S China, sometimes placed in Bytnerioideae. (Not illustrated.)

☞ - *Helicteres* Group - ☞ Subfamily Helicteroideae

At present, the subfamily includes the durian group, which may well be a proper sister group, but is preferably excluded, thus rendering the Helicteroideae as a subfamily of 8-10 genera and about 110



Eriolaena candollei, drawing adapted from WIGHT loc. cit.

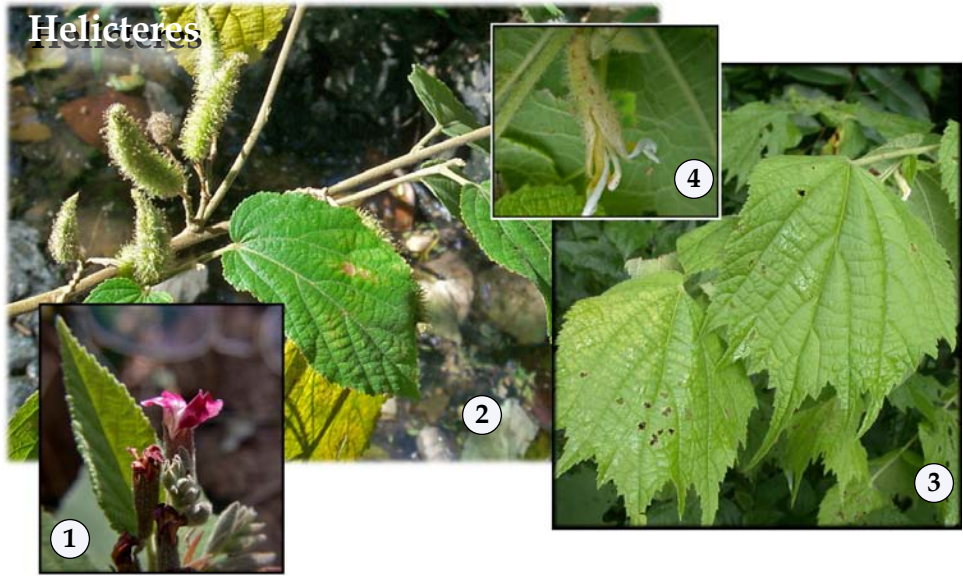
species, with 60 of these in *Helicteres*, the subfamily somewhat scattered and disjunct pantropically.

HELICTERES. [Greek, from helix, in reference to the twisted fruit] A species-rich genus of about 60 species, currently thought to be found in the seasonally dry parts of tropical Asia and tropical America. Northern Malaya claims five species. *Helicteres isora* is a small shrub with short-lived arching branches that bear bright orange flowers and the dry twisted fruit that give the genus its name, as well as the common names in most regional language. In Malay it is *kayu ules*. However, in most species the fruit are not twisted like a screw and these are represented by the most widespread species, and the only two likely found in most of the region, *H. angustifolia* and *H. hirsuta*, which are common if scattered in dry seasonal places, from India to Java and northward in the Philippines.

REEVESIA. [Commemorates John Reeves, British resident of Canton China, collector of horticultural plants.] Essentially a genus of India and S China, found south to Vietnam. The extensively cultivated *Reevesia thyrsoidea* from Hong Kong is further illustrated in THROWER loc. cit.

☞ - *Durio* Group - ☞

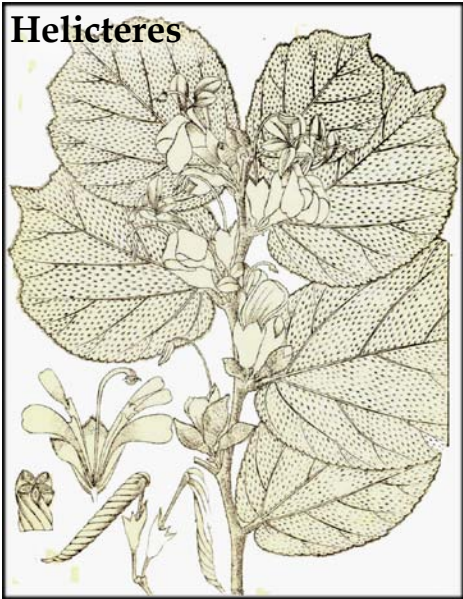
The durians and their relatives have long been misaligned with the *Bombax* trees. Recent molecular studies indicate that the nearest malvacean relatives to durians are found among the little screw-fruited shrubs of *Helicteres*, an insight marred only by the



Helicteres. 1-2, *H. hirsuta*, Philippines, small violet flowers, the petals oddly twisted and asymmetric, the fruit a hairy capsle, but not twisting as in *H. isora*; 3-4, *H. viscida*, a small shrub with arching branches, stickily pubescent leaves and small white flowers, southern Vietnam. (Photograph 2, © Leonardo L. Co.)

fact that these two genera look nothing alike. In ecology and geography they also differ in that the *Durio* Group comprises large trees of the lowland everwet forest, restricted to the Sundaic Region, whereas *Helicteres* are small shrubs and scramblers of the strongly dry seasonal lands. Also, while *Helicteres* has the 3-nerved leaf blade that character-

izes most *Malvaceae*, in the *Durio* Group we find a strongly geniculate leaf with pinnate venation, reminiscent of *Heritiera simplicifolia*. Of the *Durio* Group itself, molecular data suggests that *Neesia* is



Helicteres isora. Illustration adapted from WIGHT *loc. cit.* Note the twisted fruit that is characteristic of this species, although not of the entire genus.



Reevesia thyrsoides, illustration adapted from the original type illustration in *Edward's Botanical Register* by John Lindley, volume 15, published in 1829.

Durio

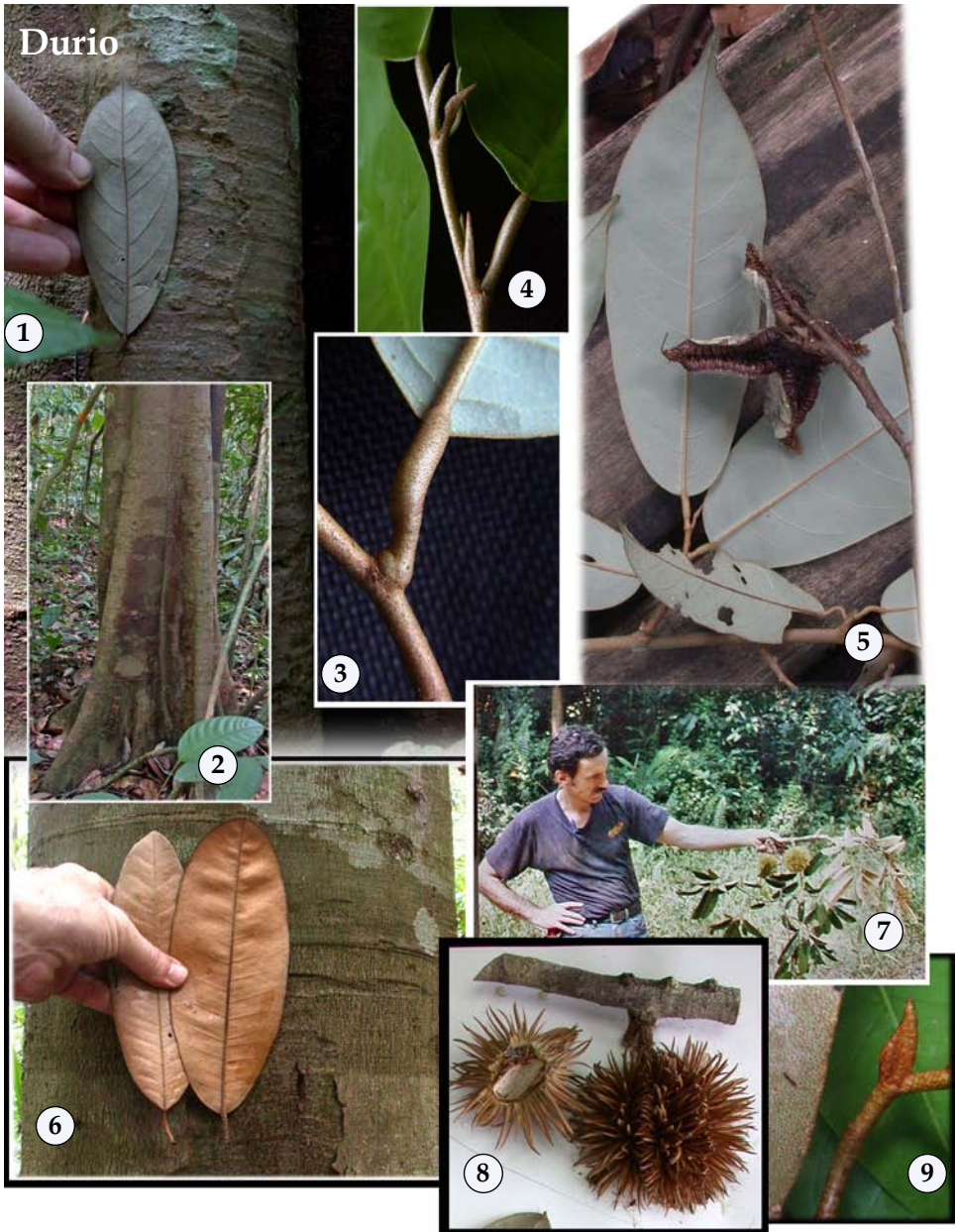


Durio. Two species of *Durio* from Lambir, Sarawak, representing two contrasting floral types. 1-3, a species related to *D. oblongus*, but differing in the smaller leaf with less pronounced nerves and the scaly red bark, possibly new; the staminal column is exceptionally long; 4-6, *D. excelsus*; 4, a weakly buttressed tree, 43 cm DBH, with red flaky bark; the large petals litter the forest floor like fallen tissue; 6, the large flowers with free spreading petals and many free stamens; 7, the fallen leaves, a glaucous white below with strongly raised nerves.

sister to the other genera, and that *Coelostegia* plus *Kostermansia* form a clade sister to *Cullenia* plus *Durio*.

DURIO. [From the Malay name, *durian*, in turn from *duri*, in reference to the thorny fruit.] The durians are almost exclusively limited to the lowland wet forests of Sundaic Region. Although there are scarcely 30 species, and these rarely appear with more than moderate abundance, the durians are such a distinctive and char-

acteristic feature of the Asian tropical forest as to be almost iconic in representing this fascinating part of the world. Consequently, I give them a bit more space than they might otherwise merit. The current accepted distribution is as follows: 20 species in Borneo, 11 in Malaya, seven in Sumatra, one endemic species in Myanmar, and two Bornean species (*D. macrophyllus* and *D. graveolens*) reaching northward into Palawan, Philippines. Those forest species that yield edible fruit are called *durian hutan* in Malay or its equivalent in other Sunda Shelf



Durio. Two species of contrasting fruit type from Pasoh, Malaya. 1-5, *D. griffithii*; 1-2 a tree of medium stature with pale pinkish bark, smooth with horizontal ridges and shallow buttresses, the leaves glaucous below with looped nerves and golden scales chiefly on the twigs and midrib; 3, the short pulvinate leaf stalk with golden scales; 4, the small sharp stipules that quickly fall away; 5, the fruit is a small capsule borne among the leaves, that dehisces on the tree, the small seeds with thin orange aril are not shown; 6-8, *D. singaporensis*; 6, the large elliptical leaves with golden lower surface the smooth trunk of the fast growing tree; 7, fruiting specimen, the fruit borne on the medium-sized branches behind the leaves; 8, the small fruit of this species, in which the seeds bear a small aril around the base of each seed; 9, from an unrelated species of *Durio*, but showing the characteristic golden scales that cover the lower leaf surface and twig apex,

languages. Those species that bear small fruits with little or no aril are given an animal epithet as in *durian burung* or *durian tupei*. Many of the individual species are sufficiently well-known to receive distinct names.

The phylogenetic structure of durians has been greatly advanced by recent molecular studies^{13,14}. The genus comprises two well-circumscribed clades: those with anthers that open by pores (sometimes segregated as *Bos-*



The photograph in the upper center shows the fruit of *Durio kutejensis* from a market in Sarawak, the species is both wild and cultivated; three other photographs of the principle commercial durian, *Durio zibethinus*, known only from cultivation, showing the creamy ivory edible aril, a market in Thailand, and the habit of the tree, with slow ripening pendent fruit and flowers borne on the thicker branches, blooming at night.

chia) and those with anthers that open by longitudinal slits (*Durio* taken narrowly.) The latter clade is further subdivided into two strongly supported clades. In the first, the filaments are fused as a staminal tube and the calyx lobes are free; in the second the filaments are free and the calyx lobes are at least somewhat fused. The advances in creating sound relationships notwithstanding,

the species level taxonomy of durians remains troubled by the poverty of collections, and the absence of soundly linked floral and fruiting material. More than most genera, the durians demand field study.

Durians are trees of medium to large stature, when large the buttresses are broad and low. The leaves are held in a plane, the lower surface covered with a layer of stellate hairs that are topped by or mixed with a layer of golden to silvery scales, the density of which varies by species. Inflorescences are borne at positions that vary by species: among the leaves, on young branchlets, on older branches or sometimes at the base of the tree. The flowers are subtended by bracts, with a deciduous epicalyx that splits as two lobes. The calyx more or less united in bud and then either splits as five free sepals or five small lobes. There are five white petals, variously large or small, numerous stamens variously free or united. The fruit is a five-locular capsule. The valves may dehisce completely on the tree or after the fruit has dropped. The seeds ellipsoid in two rows; in some species with no aril, in others the aril covers only the base of the seed or it may cover the seed is completely.

Of the commercial durian, *D. zibethinus*, little more need be said here since so much has been written elsewhere. The creamy ivory-colored aril that surrounds the seed is unique among all of the world's delectable foods. To the *aficionado*, the durian is the king of fruits.

The comparative ecology of wild durians deserves much more extensive study. Two contrasting dispersal syndromes are well-known in general. Either the fruits



Durian timber, species not noted, wood sample from the Sarawak Timber Council.

¹³Nyffeler, R. *et al.* 2000. Journal Plant Systematics and Evolution. 224: 55-82.

¹⁴Nyffeler R. *et al.* 2001. Organisms Diversity & Evolution. 1: 165-178.



Coelostegia. 1-3, *C. borneensis*, Lambir Hills, Sarawak; 1. large tree typically with great sweeping thin plank buttresses; 2. the fruit large and spiny, persistent on the ground about the tree; 3. the leaves typically dry two-tone brown with distinct golden peltate scales well-spaced on the lower surface.

open while on the tree, the aril is red or yellow and odorless, the seeds small and dispersed by birds, or in the second syndrome, the fruits open after falling to the ground, the aril is pale colored and pungent, the large seeds dispersed by mammals. Pollination is variable and includes night blooming species chiefly pollinated by bats but some perhaps also by sphingids, and day blooming species pollinated either by spider-hunters (those species with a long staminal tube) or by various large bees. Another line of ecological variation lies in the stature of the mature tree, which can be small or large. By combining the alternative strategies for dispersal, pollination and stature, each of the 30 or so species of durian has found a special way to live within the forest. The details of their individual stories are yet to be recorded.

COELOSTEGIA. [Greek, hollow-shelter, in reference to the reflexed sepals.] A genus of five species widespread in the Sundaic Region, consistent in lowland forests on rich soils although never abundant. The common names include *durian hantu* and *punggai*. These big trees are altogether fascinating in many respects. The mature tree is easily recognized from the buttresses which are wide and tall and remarkably thin, and from the fallen leaves in which the mid-rib is raised or flat above, not sunken, the leaf-stalk is kneed, the blade dries dark brown to black with well-spaced golden scales. The large fruits that look very much like durians often persist beneath the tree. The seeds are relatively small as are the arils.

KOSTERMANSIA. [Commemorates A] 'Doc' Kostermans, d 1994, Dutch botanist who spent his life in Indonesia; tireless collector, scholarly and prolific

writer.] Monotypic, *Kostermansia malayana*, a large tree found only in the Malay Peninsula, although widely there at low densities. The tree is called *durian tuang* or *krepal* in Malay. It certainly looks like a durian in the form of the leaf. (Not illustrated.)

NEESIA. [Commemorates L. Nees von Esenbeck, d. 1837.] A small genus of six to 10 species, all fairly uniform and distinctive as a genus. The Malay name is *bengang*, in Iban as *sebangkih*. These are typically trees of the mid canopy, sometimes tall with wide spreading branches from which the characteristic fruit hang, looking like *durians*. They play a trick on anyone who goes to the trouble of climbing the tree for the fruit because they are filled not with an edible aril but with small seeds and extremely irritating hairs.

These trees seem to be especially fond of damp ground, and can sometimes become relatively abundant in swampy forests. The large fruits often persist around the base of the parent trees, but also sometimes appear to wash along streams and even are occasionally found washed up along the ocean. The leaves differ sharply from *durians* in the lack of golden scales and the presence of stiff stellate hairs. Some common species such as *N. strigosa* or *N. synandra* the leaves can be mistaken for *Artocarpus*, because of their overall shape, venation, rough hairy surfaces, but the leaf stalk is slightly swollen near the upper end and the node is very different, and of course there is no white exudate in *Neesia*. BURKILL *loc. cit.* tells us that the wall of the fruit was ground and the infusion used as a diuretic.



Neesia synandra, Lambir Hills, Sarawak, the fruit spiny, 5-parted, durian-like, but splitting to release many small hair covered seeds the leaf with a long strongly pulvinate stalk, lacking 3-nerved base.

A large and taxonomically complex group of 115 genera and about 1845 species, more or less cosmopolitan. Best known by the cultivated *Hibiscus* and related food crops. The group is poorly represented among trees of tropical Asia, and scarcely at all in the lowland equatorial forests. We find nothing in Asia quite like the tropical American *Quararibea*.

CAMPTOSTEMON. [Greek for curved stamen.]

A genus comprising two closely related species of mangroves, *Camptostemon philippinense* in Borneo and the Philippines (where it is called *gapas-gapas*), and *C. schulzei* in Australia. All molecular data to date confirms that these little mangroves are related to the *Hibiscus* subfamily and were wrongly placed with the durians; they share with that group nothing more than the coppery-gold scales on the lower leaf surface.

HIBISCUS. [Classical name for the European mallow.] A pantropical genus of some 200 species. In tropical Asia, the most obvious *Hibiscus* are the numerous cultivars that are derived from varied species, Asian and American. Among the native flora we find herbs and small perennials, and also several species of trees. The most readily observed species is the ubiquitous ornamental, *Hibiscus rosa-sinensis*, native to India and grown everywhere in the tropics for the extravagant flowers that nod with casual elegance from the long twigs. Although not native to Malaya, *bunga raya* has been cultivated for

many centuries and is so well-known that it was declared the National Flower. It is also the state flower of Hawaii, although again, an obvious exotic. In the Philippines it is among the most cultivated of household shrubs; called *gumamela*, it is among the best known. The American Hibiscus Society promotes the cultivation and development of varieties which appear to be nearly infinite. The sea mallow, *H. tiliaceus*, is a medium-sized tree with yellow flowers found along all coasts of Asia, deceptively similar to *Thespesia*. Of the larger trees, the most common is probably *H. macrophylla*, also with yellow flowers, found widely along roadsides and large forest gaps; when sterile it might be easily confused with *Macaranga gigantea*. An additional 10 species of trees are in New Guinea.

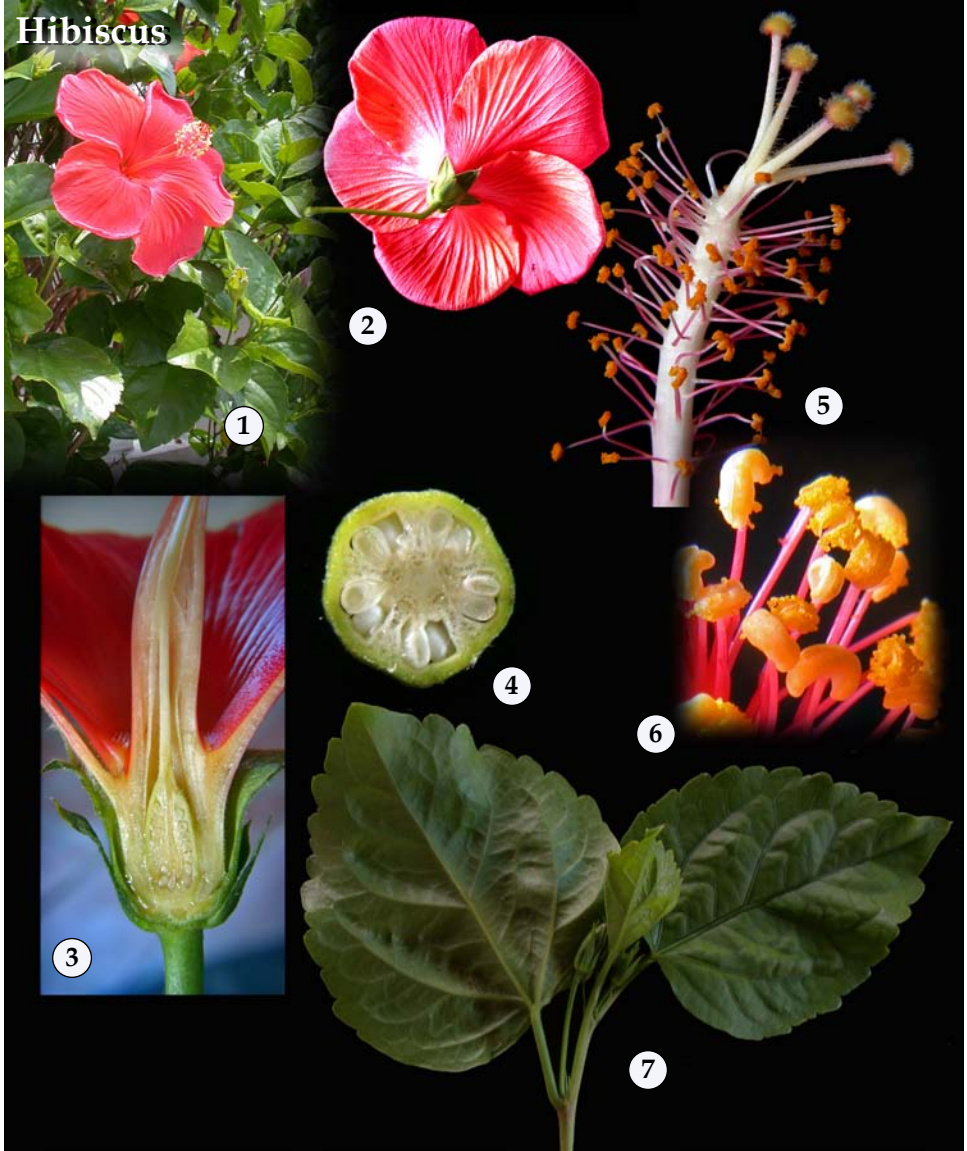
THESPESIA. [Greek, divine, in reference to the sacred status of *Thespesia populnea* in Tahiti at the time of Cook's voyage.] Pantropical, several in New Guinea, two in tropical Asia. Sometimes as *berbaru* in Malay. The most common representative is essentially one variable, widespread and abundant species, *Thespesia populnea*. However, some contend that *T. populnea* (leaves deeply cordate, fruit indehiscent, seeds with long soft hairs) differs from *T. populneoides* (leaves bronzed coppery, shallow cordate, outer layer of fruit dehiscent, seeds with short clawed hairs). *Thespesia* can be distinguished from the ecologically and morphologically similar *Hibiscus tiliaceus* by the absence of glands from the lower leaf and the shape of the fruit. *Thespesia lampas* is a widespread and abundant small shrub up to two meters tall, from E Africa to New Guinea.

ABUTILON. [From an Arabic name.] A genus of about 150, pantropical in distribution, rarely in Asia where it is chiefly represented by *Abutilon indicum*, probably originating in India and spread throughout tropical Asia in ancient times as a weedy shrub of roadsides and waste places.

KYDIA. [Commemorates Colonel Robert Kyd, founder of the Calcutta Botanic Gardens.] A genus of one variable species, *Kydia calycina*, or more finely divided, from India and China south to northern Vietnam and Thailand. Small trees of dry deciduous woodlands, with unisexual monoecious flowers. In the normal form, the leaves are woolly, while plants with nearly glabrous leaves are sometimes called *K. glabrescens*, and plants with few-flowered inflorescence and indehiscent fruit are *K. zizyphifolia*. (Also illustrated in GARDNER *loc. cit.*)

☞ - Bombax Group - ☞ Bombacoideae

A group now reduced to no more than 27 genera and about 250 species, especially Tropical America, and *Adansonia* of Africa and Australia. The group is considered close to the *Malva* group with which they share an epicalyx, a staminal tube, and numerous small seeds in capsules. It includes many im-



Hibiscus rosa-sinensis. Native to India, but cultivated everywhere in the tropical world. 1, the floral habit; 2, the overlapping petals and calyx seen from behind; 3, a transverse section of the flower showing the fusion of staminal column and petals, the epicalyx below; 4, a cross section of the ovary, numerous small seeds; 5, the staminal column with the numerous anthers spreading at different heights; 6, the anthers with pollen grains large and spiny; 7, the leaves are ragged toothed, with strong palmate venation at the base, the leaf stalk fleshy and hardly pulvinate at all.

portant trees of the American lowland equatorial forests, but they have no relatives at all in the Asian equatorial lowlands. Even *Bombax*, our sole native representative, while not uncommon in strongly dry seasonal places, is hardly a major forest component. The important genus of African trees, *Adansonia*, the baobab trees, includes one small tree native to east Australia.

BOMBAX. [Probably intended as Greek for silk in reference filling of the fruit.] Nicholson explored the

tangled history of this Linnaean genus. Paletropics, Africa to Asia. These are often large diameter trees, but not much over 30 m in height. The young trunk is usually spiny. The leaves are palmately compound, five-seven digitate, the flowers solitary or in small clusters, typically red, sometimes orange and white. They bloom when the tree is leafless. The capsule is loculicidally dehiscent with five leathery valves and the inside dense with silk wool that encloses numerous small black seeds. *Ceiba* has

Nicolson, D. 1979. *Taxon*. 28: 367-373.



Hibiscus macrophyllus, roadside in southern Vietnam.



Abutilon indicum, Philippines, a small weedy shrub, with distinctive flowers and fruit.

white flowers with five to 15 stamens, the anthers with two thecae, *Bombax* has red flowers with many stamens, each with one theca. The most widespread species is *B. ceiba*, which is now sometimes treated as *Salmalia malabarica*.

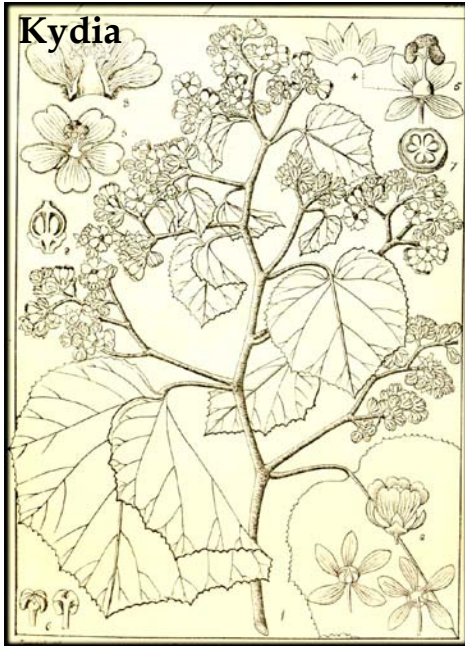
CEIBA. [From a native South American name.] Current orthodoxy sees *Ceiba* with a genus of strictly American origin with 11 species, one of which, *C. pentandra* reached Africa by long-distance dispersal in pre-human times, thence brought to tropical Asia and the Pacific in the course of early trade (MABBERLEY *loc. cit.* suggests



Thespesia



Comparison of two common and similar seaside plants of tropical Asia; on the left is *Hibiscus tiliaceus*, the calyx is rarely persistent, fruit completely dehiscent, the lower leaf surface has odd glands on the spreading palmate nerves; on the right is the similar *Thespesia populnea*, distinguished by the absence of glands from the lower leaf, the persistent calyx, and hardly dehiscent fruit. Although the leaves of the two species differ sharply in the photographs, they display an overlapping range of variation in shape and indumentum.



Kydia calycina, drawing adapted from WIGHT *loc. cit.*

500 AD?); with possibly, perhaps likely, secondary introductions from America by the Spanish and Portuguese. *Ceiba* appears to have never naturalized anywhere in

Bombax



Bombax xeiiba, illustration from BLANCO *loc. cit.*; photo of thorny trunk of juvenile from southern Vietnam.

Asia, even in places where the ecologically similar *Bombax anceps* grows freely. Very large trees can be found in many prominent locations in Asia including the Heri-



Ceiba pentandra, cultivated, the tree pictured on the right, the leaves and the open fruit are from Mt. Makiling, Philippines; the silhouette in the lower left shows the branch form, from Kuching, Sarawak.

tagi Tree in Lawn O of the Singapore Botanic Gardens, planted by Ridley in 1924, now 42 m tall and nearly two m diameter, and the illustrated tree on the padang in Kuching, Sarawak.